THE TERTIARY ECHINOIDS OF SOUTH-EASTERN AUSTRALIA

I Introduction and Cidaridae (1)

By G. M. Philip

Abstract

A revision of the Tertiary echinoids of SE. Australia is introduced. The classification of the order Cidaroida is discussed, and some changes in existing classifications suggested. The problems and uncertainties of classifying fossil cidaroids are emphasized. The following Australian Tertiary cidarids are described and figured: *Stylocidaris* (?) *scoparia* (Chapman & Cudmore), *Stylocidaris* (?) sp. cf. *S.* (?) *scoparia* (Chapman & Cudmore), *Stylocidaris* (?) *chapmani* sp. nov., *Eucidaris strombilata felli* subsp. nov., *Phyllacanthus duncani duncani* Chapman & Cudmore, *Phyllacanthus duncani gambierensis* subsp. nov., *Phyllacanthus clarkii clarkii* (Chapman & Cudmore), *Phyllacanthus clarkii impensus* subsp. nov., *Phyllacanthus serratus* sp. nov.

Introduction

Marine strata ranging from Paleocene to Pliocene in age outcrop in various parts of Victoria, South Australia and Tasmania. Echinoids collected from these rocks are in general excellently preserved, and are particularly abundant in the middle part of the record.

In the 19th century the peculiarities of the fauna and the unparalleled material excited the interest not only of Australia palaeontologists but also of such authorities as Laube, Duncan, Cotteau, Bittner and Gregory. Since then little has been written about these echinoids. The wealth of material now amassed in the collections of southern museums and universities makes the long overdue revision of the fauna a very extensive project.

It is intended that this work shall be published in a series of papers. This, the first, gives a general introduction and the first part of the systematics dealing with the Cidaridae.

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Recently Mr R. L. Foster, of Unley, S.A., has made available for study his comprehensive collection of echinoids from South Australia.

Explanatory Notes

MATERIAL, REPOSITORIES, TYPES:

This study is based largely on the collections of the National Museum of Victoria, particularly the collection of the late Mr F. A. Cudmore. Cudmore's comprehensive collection of Australian Tertiary fossils contains an unparalleled suite of echinoids. Supplementary collections of Victorian material have been obtained from:

(a) general collections of the National Museum of Victoria;
(b) Melbourne University Geology Department collections;
(c) Geological Survey of Victoria Museum.

Extensive collections of specimens from South Australian localities were obtained from:

(a) Adelaide University Geology Department collections;
(b) Mines Department of South Australia;
(c) Mr R. L. Foster, of Unley, S.A.

These different collections, together with specimens in other institutions including type specimens lodged in European museums, have necessitated the coordination of many thousands of specimens. Symbols for the catalogue numbers of the various repositories used throughout the text are:

AUGD—Adelaide University Geology Department collection, Adelaide (Prefix 'T': Tate Collection).
BM—British Museum (Natural History), London.
CPC—Commonwealth Palaeontological Collection, Bureau of Mineral Resources, Canberra.
GSV—Geological Survey of Victoria, Department of Mines, Melbourne.

MDSA—Mines Department of South Australia, Adelaide.

MUGD—Melbourne University Geology Department Type and Figured Specimen Collection, Melbourne.

P—National Museum of Victoria, Melbourne.

SM—Sedgwick Museum, Cambridge.

VNM—Naturhistorisches Museum, Vienna.

UNE—University of New England Geology Department Collection, Armidale, N.S.W.

Type specimens in the Cotteau Collection, École Nationale Supérieure des Mines, Paris, bear no registration numbers.

Some of the type specimens of the earlier species could not be located, and are apparently lost. These include the types of *Spatangus Forbesii* Woods 1862, *Echinolampas Gambierensis* Woods 1867, *Hemiaster Archeri* Woods 1867, *Echinolampas ovulum* Laube 1869, *Hemipatagus Woodsi* Etheridge 1875, and *Micraster Etheridgei* Johnston 1877. The types of *Coelopleurus paucituberculatus* and *Hemiaster planedeclivis* were stated by Gregory (1890) to be lodged in the Ipswich Museum. Mortensen (1935, p. 608) records that he instituted an unsuccessful search for the type of *Coelopleurus paucituberculatus*. Mr H. E. P. Spencer, the present curator of the Ipswich Museum, kindly undertook a further unsuccessful search for the specimens. The most serious loss is the material described by Bittner (1892). Of these specimens, Dr F. Bachmayer, Director of the Naturhistorisches Museum, Vienna, writes (2. ii. 1960)—'Die Originale von Bittner befaden sich in der Geologischen Bundesanstalt in Wien, dürften aber durch die Kriegsereignisse (Bombenschäden) zerstört worden sein. Eine Nachsuche blieb erfolglos.'

However, all but 2 of the above 16 forms can be satisfactorily interpreted from topotype material.

CLASSIFICATION:

The classification which will be used throughout is virtually that given in Mortensen's (1928-1952) monograph. Some slight modifications will be suggested at the family level of classification. Of the many changes proposed by Durham and Melville (1957) in echinoid classification, one of their innovations is deemed desirable—namely the introduction of superorder names. This is the outcome of the need to unite under one head three great orders of the sub-class Regularia—Stirodonta, Aulodonta and Camarodonta. H. L. Clark and other American authors have resolved this problem by according the groups the rank of suborders in the order Centrechinoida (as they were originally proposed by Jackson), but it seems desirable to recognize the categories as orders in harmony with Mortensen's classification. The superorder Diadematacea may be employed, emended from the usage of Durham and Melville (1957), to include the orders Stirodonta, Aulodonta and Camarodonta as used by Mortensen. As the classification of echinoids will be discussed elsewhere, this is the only point which needs explanation here.

TERMINOLOGY:

Echinoid terminology requires no explanation. Glossaries and definitions of descriptive terms are given in various papers (e.g. Bather 1909, Jackson 1912, Grant and Hertlein 1938, Fell 1954, Cooke 1959) or text books (e.g. Morley Davies 1935). In the description of the regular echinoids the usual abbreviations h.d. (horizontal diameter) and v.d. (vertical diameter) are employed for the dimensions of the test. The nomenclature for the orientation of the test is that of Lovén (1874).

The generic synonymies are abbreviated, as a full treatment of the older literature has been given by Mortensen (1928-1952). Some attempt is made to list the major contributions since Mortensen's monograph. With the genera discussed the type species is named and the nature of its selection indicated.

Full synonymies are given for the various species. Listed are all references which include either descriptions, figures, changes in nomenclature, or any new information appertaining to the species. Thus mere mentions in faunal lists have been omitted. However, although many of the references in H. L. Clark's (1946) survey of Australian echinoderms amount to no more than a listing, because of the importance of Clark's monograph these are all included in the present synonymies.

For the sake of brevity titles of papers, etc. have been omitted from the synonymies.

ILLUSTRATIONS:

The text-figures of echinoids for this study were prepared directly from specimens, either with the aid of a *camera lucida* or a binocular microscope with a graticuled eyepiece.

In the photographic illustrations an attempt has been made to represent the variation of the various species, and also to document occurrences from widely separated localities. Because of the large number of figures, measurements have been kept to a minimum, except where they assist discrimination of forms.

Historical Account

The first record of the occurrence of Tertiary echinoids, indeed, of marine Tertiary invertebrates, in SE. Australia was by Captain Charles Sturt (1834) in the journal of his voyage of exploration down the Murray River. He listed and figured a suite of fossils collected from the cliffs along the Murray River. The echinoids included:

Scutella sp.   (= *Monostychia australis* Laube)
Spatangus Hoffmanni Goldfuss
                                  (= *Lovenia forbesii* (Woods))
Echinus   (= '*Psammechinus*' *woodsi* Laube)

Although Tertiary echinoids were mentioned in the earlier writings of Tenison Woods, it was not until 1862 that the first species was described, and then its proposal appears to have been unpremeditated. Woods published two figures of a spatangoid bearing the caption '*Spatangus Forbesii*, Mount Gambier'. The first of these is unrecognizable, while the second is a direct copy of Sturt's (*op. cit.*) figure of his *Spatangus Hoffmanni* from the Murray Cliffs, published without acknowledgement. There is no indication that Woods considered his '*Spatangus Forbesii*' to be a new species, and, indeed, later articles published by Woods and McCoy would indicate that Woods had inadvertently published a museum manuscript name used by McCoy. Woods also gave figures of a form he identified as *Echinolampas* and indicated the occurrence of *Cidaris* and *Cardiaster* at Mt Gambier.

In 1864, Duncan, in his first contribution on the Australian Tertiary echinoid fauna, redescribed *Spatangus Forbesii* Woods as '*Hemipatagus Forbesi* (Woods and Duncan)' and recorded the species *Clypeaster folium* Agassiz (= *Monostychia australis* Laube). In 1867, Tenison Woods described from Mt Gambier *Echinolampas Gambierensis* sp. nov., *Hemipatagus Forbesi* (accepting Duncan's citation of

the species) and *Hemiaster Archeri* sp. nov., the last being the form illustrated as *Echinolampas* in 1862.

The first significant contribution to the description of the fauna was made by Laube (1869). From the Murray River Cliffs he described:

> *Psammechinus Woodsi* sp. nov.
> *Paradoxechinus novus* gen. et sp. nov.
> *Monostychia australis* sp. nov.
> *Catapygus elegans* sp. nov.
> *Echinolampas ovulum* sp. nov.
> *Micraster brevistella* sp. nov.
> *Eupatagus Wrighti* sp. nov.
> *Eupatagus Murrayensis* sp. nov.
> *Hemipatagus Forbesi* (Woods).

In 1875, Etheridge described the common spatangoid from Beaumaris, Victoria, as *Hemipatagus Woodsi* sp. nov., but this he abandoned subsequently (1878) as a variety of *H. Forbesi,* in deference to the views of Duncan.

Duncan (1876) described a large number of species from many localities in Victoria and South Australia. As new, he proposed:

> *Leiocidaris Australiae* sp. nov.
> *Temnechinus lineatus* sp. nov.
> *Arachnoides Loveni* sp. nov.
> *Arachnoides elongatus* sp. nov.
> *Rhynchopygus dysasteroides* sp. nov.
> *Echinobrissus Australiae* sp. nov.
> *Holaster Australiae* sp. nov.
> *Maretia anomala* sp. nov.
> *Eupatagus rotundus* sp. nov.
> *Eupatagus Laubei* sp. nov.
> *Megalaster compressa* gen. et sp. nov.
> *Lovenia Forbesi* var. *minor* var. nov.

and identified the following exotic species:

> *Schizaster ventricosus* Gray
> *Echinanthus testudinarius* Gray
> *Echinarachnus parma* Gray
> *Pygorhynchus Vassali* Wright.

Tate, in 1877, described the species *Salenia tertiaria*. In that year Johnston diagnosed *Micraster Etheridgei* from Tasmania.

Etheridge (1878) gave a check list of described species and introduced the name *Echinolampas australis,* attributed to Tenison Woods, and seemingly a *lapsus calami* for *E. gambierensis* Woods.

McCoy (1879, 1882), described and figured a number of forms. As new species he proposed:

> *Clypeaster gippslandicum*
> *Pericosmus gigas*
> *Pericosmus Nelsoni*
> *Lovenia Forbesi*
> *Pericosmus compressus.*

This last he thought might be conspecific with Duncan's *Megalaster compressa.*

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Pomel (1883) proposed the genera *Corystus*, based on *Rhynchopygus dysas-teroides* Duncan, and *Pleurosalenia* for *Salenia tertiaria* Tate.

Tate (1885b) described *Fibularia gregata* sp. nov. and *Linthia antiaustralis* sp. nov. without, however, providing figures.

Duncan, in 1887, gave an account of the composition of the Australian Tertiary echinoid fauna. He proposed the genus *Ortholophus*, based on *Temnechinus lineatus*, and a new variety, *Clypeaster folium* var. *elongata*. He also introduced the name *Holaster difficilis* to replace *Rhynchopygus dysasteroides*, as he had misinterpreted this species.

Tate (1888) reviewed the generic composition of the Australian Tertiary echinoid fauna and published the manuscript generic name *Murravechinus*. This he later stated (1891, p. 274) was based on *Coelopleurus paucituberculatus* Gregory, 1890.

Duncan (1889) mentioned a number of the Australian species, and instituted one change. The subgenus *Studeria* was proposed for *Catapygus elegans* Laube.

Gregory (1890) described and figured the following forms:

> *Cassidulus longianus* sp. nov.
> *Echinolampas posterocrassus* sp. nov.
> *Cardiaster tertiarius* sp. nov.
> *Coelopleurus paucituberculatus* sp. nov.
> *Hemiaster planedeclivis* sp. nov.

Also Gregory considered that *Megalaster compressa* Duncan and *Pericosmus compressus* McCoy were different species of *Pericosmus*, and proposed *P. M'Coyi* nom. nov. for McCoy's species. However, the form he figured was not *P. compressus* McCoy.

Cotteau (1890-1891) described the following species from Mt Gambier:

> *Echinolampas Morgani* sp. nov.
> *Galeraster Australiae* gen. et sp. nov.
> *Cyclaster Morgani* sp. nov.
> *Gualtieria Australiae* sp. nov.
> *Scutellina Morgani* sp. nov.

Tate (1891) summarized the history of the description of the Tertiary echinoids and provided partial synonymies for most forms then described. He proposed the new species:

> *Salenia globosa*
> *Scutellina patella*
> *Echinobrissus Vincentinus*
> *Cardiaster latecordatus*
> *Schizaster abductus*

Tate also noted that Gregory's illustrated specimen of *Pericosmus compressus* Mc-Coy was not correctly identified, and proposed the name *Eupatagus decipiens* for it.

Bittner (1892) described a large suite of Tertiary echinoids sent by Tate to Vienna on exchange. He proposed as new:

> ?*Psammechinus humilior* sp. nov.
> *Psammechinus Woodsi* var. *fascigar* var. nov.
> *Coptechinus lineatus* sp. nov.
> *Coptechinus pulchellus* sp. nov.

Fibularia gregata var. *orbiculus* var. nov.
Fibularia Tatei sp. nov.
Progonolampas Novae-Holandiae gen. et sp. nov.
Cyclaster lycoperdon sp. nov.
Australanthus gen. nov. (for *Cassidulus longianus* Gregory)
Tristomanthus gen. nov. (for *Catopygus elegans* Laube).

Tate (1892) strongly criticized Bittner's 'forcible efforts at species making', and concluded that not one of the new forms described by Bittner was valid. (In fact, Bittner was maligned by Tate for the majority of his species were well founded.) In the same year Gregory described *Cassidulus florescens* sp. nov., and removed Tate's *Eupatagus decipiens* to *Macropneustes*.

Tate (1893) described 4 new species:

Arachnoides incisa
Conoclypeus rostratus
Laganum platymodes
Sismondia murravica.

In 1896 Lambert proposed the genus *Duncaniaster,* based on *Holaster australiae* Duncan.

Tate (1898) again reviewed the Australian Tertiary echinoid fauna, the only important changes being that he placed his *Conoclypeus rostratus* in the genus *Pleisiolampas,* and gave *Macropneustes decipiens* (Tate) as a species of *Meoma.*

Hall (1907) described the new species:

Echinoneus dennanti
Prenaster aldingensis
Brissopsis Tatei
Schizaster sphenoides.

Chapman (1908) illustrated a specimen from Curlewis identified as *Linthia antiaustralis* Tate, and gave some new occurrences of previously described species. In the same year Pritchard diagnosed the new species *Linthia mooraboolensis* and placed *Pericosmus gigas* McCoy and *P. nelsoni* McCoy in *Linthia.* Chapman (1913) figured a specimen identified as *Echinocyamus* (*Scutellina*) *patella* Tate. In 1914, he illustrated a number of Tertiary echinoids. In 1917, he described a new species of foraminifera, *Bolivina hentyana,* which has been shown to be based on either a scrobicular or miliary radiole of a cidarid (Jenkins 1958). And in 1923, he figured a pebble which he took to be the internal mould of an echinoid which he identified as 'cf. *Lovenia*'.

The profound changes in echinoid nomenclature wrought by Lambert and Thiéry (1909-24) caused a general re-shuffle of the generic position of the Australian species. They proposed the taxa:

Fossulaster Halli gen. et sp. nov. for the form illustrated as *Scutellina* sp. by Hall (1908). *Progonolampas Tatei* sp. nom. nov. for *Conoclypeus rostratus* Tate, a homonym of *Echinolampas rostratus* Cotteau.

Lambert (1920) also diagnosed the genera *Granobrissoides* for *Gualtieria australiae* Cotteau, and *Victoriaster* for *Pericosmus gigas* McCoy.

Chapman and Cudmore (*in* Chapman 1928; Chapman and Cudmore 1934) described the cidarids of the fauna. They proposed the species:

Phyllacanthus duncani
Prionocidaris scoparia

Chondrocidaris clarkii
Goniocidaris prunispinosa
Goniocidaris pentaspinosa
Goniocidaris murrayensis
Goniocidaris mortenseni.

Brighton (1929a) illustrated the ambulacral structure of the holotype of *Cardiaster tertiarius* Gregory.

Mortensen (1928-1952), in his monograph of the class, mentioned a number of Australian Tertiary species, particularly type species of genera.

H. L. Clark (1946), in his review of the echinoderm fauna of Australia, gave partial synonymies of most of the Tertiary echinoid species, altering the generic placement of some.

Fell (1949) described a temnopleurid from the Murray River Cliffs, South Australia, as *Brochopleurus australiae* sp. nov. Fell (1953) also gave a generalized account of the generic composition of the Australasian Tertiary echinoid fauna, and also reviewed the Australian Tertiary cidarid fauna in his description of the Cainozoic cidarids from New Zealand.

Durham (1955) illustrated the plating for the species *Monostychia australis* Laube and *Sismondia murravica* Tate, gave figures of *Fossulaster halli* Lambert and Thiéry, and diagnosed the genus *Scutellinoides* based on *Scutellina patella* Tate.

More recently, the present writer (1957) described the plating structure of *Lovenia woodsi* (Etheridge), the peculiarities of which had been noted by Hawkins (1916).

Two minor inaccuracies have arisen concerning the fauna. Lambert and Thiéry (1914, p. 310) list the living species *Anomalanthus tumidus* (Woods) (currently regarded as a species of *Clypeaster*) as occurring in the Pliocene of Australia, a statement apparently followed by Stefanini (1924). The Miocene species *Lovenia woodsii* (Etheridge) is considered by Cotteau (1878, p. 215) to be living.

Excluding *nomen nuda,* a census shows that 83 nominal species and varieties have been proposed for Tertiary echinoids of SE. Australia, of which about 50 species are currently regarded as valid (H. L. Clark 1946 lists 52); the type specimens of over half of the nominal species and varieties were lodged in extra-Australian museums; in all 18 generic or subgeneric categories have been proposed, based on type species from this Tertiary fauna.

Systematics

Subclass REGULARIA

Order CIDAROIDA Claus

INTRODUCTION:

Cidaroids are notoriously unamenable to systematic treatment, bringing with them their own peculiar problems. The stereotyped features of the test and radioles within the order has in the past given rise to considerable uncertainties in classification.

To Mortensen (1903 and subsequently) is owed the present classification of living cidaroids. Among other features, Mortensen placed much taxonomic importance on the nature of the pedicellariae and spicules of the intestinal wall,

details which had largely been overlooked by earlier workers. Although Mortensen's classification originally met with considerable criticism from contemporary zoologists, it has now come to be accepted for the arrangement of living forms.

Palaeontologists, however, have not been so unanimous in following Mortensen's work. A criticism is expressed by Cooke (1946, p. 199) who writes—'More recent authors, particularly Mortensen (1928), have split the natural genus *Cidaris* into innumerable so-called genera, basing them on trivial differences that appear to be at the most subgeneric or even merely specific variations. The Cidaridae should be restudied by someone who has access to both Recent and fossil species and who has a better sense of proportion in the evaluation of morphological features.' The same writer has expressed a similar, although less emphatic view subsequently (Cooke 1953, p. 5; 1957, p. 7).

In this appraisement of Mortensen's work it is necessary to dissociate two very different bases of criticism.

The first appears to arise from the familiar dichotomy between the classification of the palaeontologist and that of the zoologist—the former of necessity deals only with the hard parts or those which survive on fossilization. Mortensen's work has provided the only reasonable subdivision of living forms. That it cannot be used readily in classifying fossil cidaroids is no valid criticism of the classification, but a limitation of the fossils (although it was for this very reason that Lambert and Thiéry (1909, 1910) rejected Mortensen's classification). Indeed no fault can be found in the basis of Mortensen's classification of cidaroids, as his work, considering as it did the total animal, provides the only possible rational subdivision. That his classification emphasized minutiae not usually found in fossil forms was the outcome of the fact that gross morphology within the groups allows of only slight indication of affinities.

The other criticism contained in Cooke's comment is directed at the level of Mortensen's classification. What is to be said here, however, cannot be said as criticism, but more as explanation. Mortensen's searching taxonomy of living echinoids was directed at distinguishing the slightest of variations. These variants invariably were then distinguished as species. His taxonomy was, of necessity, what Mayr, Linsley and Usinger (1953) would term 'alpha taxonomy'—'the distinguishing, identifying, describing, and naming of species', upon which foundation will eventually be based a complete classification.

In most branches of taxonomy polytypic species are recognized, and in the growing synthesis of taxonomy, this procedure is extending to more and more groups. Mayr (1954) offers a penetrating analysis of Mortensen's taxonomy. He notes that 'Allopatric populations are generally ranked by Mortensen as full species' and that it is 'evident that many of the so-called "species" would be called subspecies in other branches of taxonomy . . . The fine splitting on the species level affects classification on the higher level. Most polytypic species or superspecies are treated by Mortensen as separate genera.'

Nowhere is this more obvious than in Mortensen's generic subdivisions of the living cidarids. For example, he recognized (1928) 5 subgenera of *Goniocidaris* through which were distributed 14 living species. These may well be grouped as 5 (or perhaps 6) 'good' polytypic species, which practice leads to simple nomenclature which adequately defines the relationships of the different forms.

Although a synthesis of the work of Mortensen requires considerably more information on distribution than is at present available (a surprising number of nominal species are known from one or two specimens dredged from a particular

locality), and should entail detailed study of the forms in question, nevertheless in dealing with living genera the obvious species groups have been given. This is done so that the generic level of classification can be recognized at least approximately.

SUBDIVISION OF THE ORDER:

Mortensen (1928) divided the cidaroids into 2 families—the Palaeozoic Archaeocidaridae and the Mesozoic to Recent Cidaridae. This latter family was further split into 3 subfamilies. These were the Streptocidarinae for the early Mesozoic imbricate cidaroids, and the Stereocidarinae for the remainder of the Mesozoic to Recent cidaroids, except the peculiar Mesozoic genera *Diplocidaris* and *Tetracidaris,* which were set apart in the subfamily Diplocidarinae. The subfamily Stereocidarinae was further subdivided into 7 groups.

Durham and Melville (1957) would accord the subfamilies Stereocidarinae and Streptocidarinae, as used by Mortensen, the rank of independent families (Cidaridae and Miocidaridae respectively), a change which is almost inevitable following the present-day trend of the upgrading of hierarchy in invertebrate classification. However, Durham and Melville would also recognize Mortensen's 7 groups as subfamilies of the Cidaridae, 'as also the family Psychocidaridae Ikeda', which changes are open to serious criticism. This is particularly obvious in the suggested treatment of the Psychocidaridae.

The family Psychocidaridae contains the single monotypic genus *Psychocidaris,* described by Ikeda (1935) from the Bonin Islands. The major features which distinguish this genus from other cidaroids are:

(a) Imperforate primary tubercles. Of the cidaroid genera discussed by Mortenson (1928) the Cretaceous genus *Typocidaris* alone has this feature. It may now well be included in the Psychocidaridae.
(b) No interradial peristomial plates are present in *Psychocidaris.*
(c) The globiferous pedicellariae lack true poison glands and are thus intermediate in structure between those of the cidarids and other regular echinoids (Ikeda 1939c).
(d) The modified cortex layer (if, indeed, it can be called such) of the radioles is similar in structure to the radiating lamellae, and quite unlike the dense cortex layer of the cidarids.

So marked are these distinctions (in many features the form is intermediate between the cidarids and the saleniids), that Mortensen (1951, p. 555) was prepared to accept the family as co-ordinate with his Archaeocidaridae and Cidaridae. Certainly the family has no place among the ill defined groups which were recognized by Mortensen within his usage of the subfamily Stereocidarinae.

As the classification of Mortensen (1928) is no longer fully acceptable, 4 families may be recognized within the order Cidaroida. These are:

Archaeocidaridae McCoy
Cidaridae Gray (= Stereocidarinae Lambert of Mortenson 1928 + Diplocidarinae)
Psychocidaridae Ikeda
Miocidaridae Durham and Melville (= Streptocidarinae Lambert of Mortensen 1928).

The Miocidaridae is by far the most ill defined family and perhaps should merely be considered as a subfamily of the Cidaridae. It includes principally Triassic genera,

and (as the subfamily Streptocidarinae) was distinguished by the imbrication of coronal plates by Lambert (1900) and Mortensen (1928). Bather (1909, p. 88) has pointed to the fact that even in typical genera such as *Triadocidaris* there is a tendency for the imbrication to be lost. Mortensen includes in the group such genera as *Mikrocidaris* and *Aplocidaris* which apparently possess rigid tests. Furthermore imbrication is seen in young specimens of some living cidarids (e.g. *Austrocidaris canaliculata* (Agassiz), Döderlein 1887, Pl. 9, fig. 6). But as typical miocidarids represent an important stage in the derivation of the cidarids from the archaeocidarids, the family may be retained in this phylogenetic context, although taxonomic difficulties accompany its recognition.

The other families are well marked both morphologically and phylogenetically and need no further explanation.

Next, the subfamily arrangements within the Cidaridae must be discussed. As noted above, Durham and Melville would recognize Mortensen's (1928) groups as subfamilies. These however are virtually the end groupings to a key of the structure of the pedicellariae and, furthermore, are of very different value, so that they most certainly cannot all stand in formal classification, although they are of use in identifying living cidarids from the pedicellariae.

Indeed, any attempt at natural subdivision of the Cidaridae is fraught with uncertainty, and for this very reason no acceptable categories have been proposed within the family. Despite this, when considering the gross features of the test, the radioles, the geological history and, in living groups, the pedicellariae and the character of the spicules of the intestinal wall, a threefold subdivision of the family presents itself. Whether or not these groups can be considered as subfamilies of the Cidaridae is a matter for future study. They are:

SECTION I (Group Histocidarina Mortensen 1928)— Inner distally directed processes on the inner peristomial plates; cortical hairs of the radioles simple or wanting; tubercles deeply crenulate; pores non-conjugate; globiferous pedicellariae absent; spicules of the intestinal walls small and almost wanting.

Mortensen (1928, p. 69) comments that this group stands so apart from the rest of the cidarids 'that it might perhaps rather be justified to regard it as a separate subfamily'. This, however, is not said of any of his other groups.

SECTION II (Groups Cidarina, Stylocidarina and Rhabdocidarina of Mortensen 1928)—Tubercles smooth or crenulate; pores non-conjugate or conjugate; cortical hairs of the radioles usually well-developed; globiferous pedicellariae specialized, usually with a well differentiated terminal opening and often with projecting rods on the stalk; spicules of the intestinal wall small glassy plates.

Mortensen (1928) distinguished his 2 very similar groups the Cidarina and the Stylocidarina by the presence or absence of an end tooth in the larger globiferous pedicellariae. It should be pointed out that H. L. Clark (1907) figured a specimen of *Tretocidaris bartletti* (Agassiz) in which both types of globiferous pedicellariae were present. Indeed, on the basis of this, Agassiz and Clark (1907) went so far as to deny the classificatory value of pedicellariae. Mortensen (1909, p. 47; 1928, p. 316) maintained that the specimen concerned was a hybrid. This does not alter the fact that the 2 groups, to be distinguished merely by these pedicellariae, must be very closely related. On the other hand, the Rhabdocidarina is better characterized but intergrades with the Stylocidarina through the genus *Prionocidaris*.

SECTION III (Groups Stereocidarina, Goniocidarina and Ctenocidarina of Mortensen 1928)—Often small forms, usually with smooth tubercles and invariably with non-conjugate pores which may be oblique; sutures often pitted or incised, particularly those of the interambulacra; radioles usually with well-developed cortical hairs; globiferous pedicellariae simple or generalized in structure; spicules of the intestinal wall triradiate.

This group appears to be natural although it is almost impossible to define in terms of test characters. There seems little doubt from the evidence of the Australian Tertiary forms that the Goniocidarina and Ctenocidarina arose from the Stereocidarina in the late Palaeogene. All 3 groups possess distinguishing features of the test which allow their confident recognition. However, in tracing the groups backward in time the characters are found to intergrade and the groups to converge and lose their identity. This will be discussed in detail in Part II.

The subfamily Diplocidarinae, characterized by biserial ambulacra (a feature seen to some extent in other Mesozoic cidaroids), would seem to be of value comparable with these compounded groups.

FOSSIL CIDARIDS:

Because of the intractable generic taxonomy of fossil cidarids two superficially very different approaches have arisen. Purely artificial 'generic' classifications such as those of Lambert and Thiéry (1910) and Gignoux (1933) have been proposed. These are based on gross features of the test which have long since been recognized as of little value in the subdivision of living species.

The other approach, seen notably in the work of Chapman and Cudmore (1934) and Fell (1954) working on Cainozoic faunas, is to endeavour to recognize in fossil forms features which give indications of affinity with living genera. The danger here is that the living genera should be employed merely as 'form genera' with their identification based on but a single attribute (radioles with cup-shaped terminations = *Goniocidaris*; radioles with thorns = *Prionocidaris*; radioles with flanges = *Chondrocidaris*, etc.). This can lead to a taxonomy as unsatisfactory as that of the first procedure. Despite this, it is often possible to arrive at a fairly definite opinion of the generic affinities of many of the Australian Tertiary species from a detailed study of the living Indo-Pacific cidarids. But it should be emphasized that, because of the inherent uncertainty of the taxonomy, the procedure must lead to a very broad interpretation of some genera.

The classification of fossil cidarids brings other problems.

The first of these is the uncertainty in correctly associating isolated radioles with isolated test fragments. The convincing association of test and radioles is known in only two of the many forms described below. Often, however, from the one locality test fragments and radioles may be known which show reasonable indications of belonging to the same genus, and hence to the same species. In the more abundant forms the association may be indicated by the fact that certain radioles are co-extensive with fragments of a particular test. The reasons for the association of test and radioles in the various species are given in full.

Furthermore, there is the problem of what treatment is to be accorded forms known only from radioles. Here there is room for some doubt. At one extreme Hawkins (1934, p. 159) stated of some fossil cidarid radioles from Fiji—'But the taxonomic value of a cidarid radiole (at least in fossil material) is very slight, and,

though I still consider these to represent a true *Phyllacanthus,* I lay no stress on their resemblance to those of living species'. On the other hand, Fell (1954, p. 10) considered that—'Isolated, even fragmentary radioles can provide valuable informa-tion' and 'They should be regarded as legitimate material for taxonomic palaeon-tology . . .'. Bather (1909) is perhaps the most judicious in his stand on the naming of incomplete echinoderm remains. He writes (p. 7)—'As regard the application of specific names to such fragments, it seems to me that, if our descriptions are to be of practical service to stratigraphers, then they must be accompanied by names. A des-cription without a name is soon lost sight of, whereas a name compels attention until at last it finds its proper place, if only as a synonym.'

The point then would seem to be that fragments should be of some possible stratigraphic service before their naming is justified.

Thus the systematic treatment here differs considerably with the nature of the material. Where the material adequately indicates the generic affinities of the form concerned, or is widespread, systematic categories have been introduced. Where the material is inadequate to define the characters of the species, or its generic relations are obscure, or the material is poorly or inadequately located, usually open nomen-clature has been used. Often within the species informal varieties (usually based on the differences in the radioles in specimens from different horizons) have been recognized, and these may eventually prove worthwhile as formal taxonomic cate-gories.

AUSTRALIAN TERTIARY CIDARIDS:

The Tertiary cidarids of SE. Australia comprise a very important part of the whole echinoid fauna, both in number of species and relative abundance. Whereas in Europe the family flourished in the late Mesozoic and is poorly represented in both the Tertiary and Recent faunas, it would seem that rather the opposite applies to its history in the Indo-Pacific and Australasian regions (although there is still but little information available concerning Mesozoic echinoids). The Recent echinoid fauna of the Indo-Pacific contains over nine-tenths of the known living cidarids, so it is not surprising that Tertiary representatives of no fewer than one third of the living genera have to date been recorded from the Australasian region.

Chapman and Cudmore (1934), in their account of the Tertiary cidarid fauna of SE. Australia, brought together a collection of some 3000 radioles and some 400 test fragments. In the course of the present study their material has been critically examined, together with further specimens collected subsequently. Chapman and Cudmore, in their taxonomy of these difficult echinoids, had very little conception of the limits of their 8 species, although they recognized the main generic elements of the fauna. The difficulty they encountered in delimiting their species can be seen in the labelling of collections within the National Museum, Melbourne. In their interpretation of *Stereocidaris australiae* (Duncan) they included in part the tests of 9 well-marked species; if radioles are also considered then the number of species is about 15. Thus, their records of species from the various localities are untrust-worthy. Throughout it is attempted to give synonymies of Chapman and Cudmore's species as they used them in their museum labelling; this, however, gets extremely involved in some species, and so the synonymies must be regarded as fully reliable only in the treatment of the figured material.

As Chapman and Cudmore's paper includes illustrations of a considerable num-ber of different cidarids, for reference a re-identification of their figured specimens is given in Table 1.

TABLE 1

	Chapman and Cudmore's (1934) identifications of figured cidarids	Identifications herein
Fig.		
1–3	*Stercacidaris oustroliae* (Duncan)	*Stcrcacidaris* sp. nov. A
4	,, ,,	*Stercacidaris* sp. nov. B
5–6	,, ,,	*S. australiae* (Duncan)
7*–8	*Phyllacanthus duncani*	*P. duncani* C. & C.
9	,, ,,	*P. clarkii* (C. & C.)
10*	*Prionacidaris scoporio*	*Stylocidoris* (?) *scoporia* (C. & C.)
11	,, ,,	*Phyllocanthus duncani* C. & C.
12*–14	*Ganiacidaris prunispinosa*	*Stercacidaris* (?) *prunispinosa* (C. & C.)
15–17*	*Chandracidaris clarkii*	*Phyllacanthus clarkii* (C. & C.)
18–19*	*Goniocidoris pentospinosa*	*G. pcntaspinosa* C. & C.
20–22*	*G. murrayensis*	*G. murroyensis* C. & C.
23*	*G. mortenseni*	*G. tubaria martenseni* C. & C.
24	'Smooth Spines, *incertoe sedis*'	*Radiolus* sp. 1
25–26	'Club-shaped Spines, *incertoe sedis*'	*Eucidaris strombilato fclli* subsp. nov.
27	*Ganiocidaris mortcnseni*	*G. tubaria mortenscni* C. & C.
28–30	*Prianocidoris scapario*	*Stylocidaris* (?) *scoporio* (C. & C.)
31	*Chondrocidaris clarkii*	*Radiolus* sp. 2
32	*Stereocidaris oustraliae*	*Stereocidaris* sp. nov. C
33	*Phyllacanthus duncani*	*P. duncani* C. & C.
34–35	*Stereocidaris austrolioe* (Duncan)	*Radiolus* sp. 6
36a–b	,, ,,	*Radiolus* sp. 7
36c	,, ,,	*Radiolus* sp. 8

* Type specimen, or including type specimen.

Family CIDARIDAE Gray

Genus Stylocidaris Mortensen

Stylacidoris Mortensen 1909, p. 52.
Stylacidaris Mortensen 1928, p. 334 *et. scq.* (*cum synon.*)

TYPE SPECIES: *Cidaris affinis* Philippi, by original designation.

DIAGNOSIS: Comparatively large forms with non-conjugate pores and smooth or crenulate tubercles. Radioles usually with simple terminations and ornamented with granules or serrated ridges. Cortical hairs usually simple.

REMARKS: The extremely generalized and uniform character of tests and radioles in both the Stylocidarina and Cidarina does not allow distinction between the groups in dealing with fossil material. As the Cidarina is at present typically a Mediterranean and Atlantic group (first recognized in the Indo-Pacific by Mortensen 1939), it seems best to regard the forms in this fauna which have such generalized characters as belonging to the Stylocidarina rather than the Cidarina. Two species fall within this category, but even so, neither of them can be regarded as fully typical of *Stylocidaris*. The peculiarities of each are discussed below after their descriptions.

DISTRIBUTION: The genus is cosmopolitan in the present-day seas, although it is far more common and diversified in the Indo-Pacific than elsewhere. Mortensen (1928) recognized 18 species and subsequently (1932, 1939) described 2 more species and a variety. These numerous named forms may be arranged in 5 species groups, the relationships within which are complex, particularly in the first. These are: *S. affinis* (Philippi)—*S. reini* (Döderlein), *S. annulosa* Mortensen, *S. calacantha* (Agassiz and Clark), *S. bracteata* (A. Agassiz), *S. tiara* (Anderson).

S. rufa Mortensen and *S. fusispinina* Mortensen are not certainly species of *Stylocidaris*.

Stylocidaris (?) scoparia (Chapman & Cudmore)
(Pl. XXI, fig. 1-2, 4-8; fig. 1a, 2b)

Prionocidaris scoparia Chapman and Cudmore 1934, p. 134-135 (*partim*), Pl. 12, fig. 10 (*non*) fig. 11; Pl. 15, fig. 28-30; H. L. Clarke 1946, p. 256 (*partim*); Fell 1954, p. 11 (*partim*).

DIAGNOSIS: Test large, with narrow ambulacra, narrow interambulacral midzones and large, smooth tubercles. Scrobicular tubercles prominent and overhanging, with inner ridges resembling those of *Phyllacanthus*. Interporiferous tract narrow and ornamented by a regular series of large, almost contiguous marginal tubercles which on each plate are supplemented usually by 2 small internal tubercles. 7 interambulacral plates in each vertical series and 16 ambulacral plates opposite the highest interambulacral plate.

Radioles large and cylindrical, with shafts ornamented by irregular, distant thorns, and the distal termination may be flared and flattened. Collar long and milled ring markedly expanded.

TYPE SPECIMEN: Chapman and Cudmore's (Pl. 12, fig. 10) syntype from Aldinga (AUGD T360), a test with a detached radiole lying across the apex, is here designated lectotype. Dr Mary Wade, University of Adelaide, kindly examined the specimen and considered it to have come from the Port Willunga Beds (Janjukian to Batesfordian).

Chapman and Cudmore's other syntype (P13709) is a specimen of their *Phyllacanthus duncani*.

DESCRIPTION: The test is large and depressed with slightly incised ambulacra, and a peristome comparable in width to the apical system.

The slightly sinuate ambulacra are narrow, about 15% of the width of the interambulacra. The poriferous tract is slightly sunken and almost twice the width of the interporiferous tract. The non-conjugate pores are large and somewhat slit-like, with the wall between rising to a low elevation (Fig. 1a). The transverse ridge above the pores is fairly well developed. The interporiferous zone is ornamented by a regular series of large, almost contiguous, marginal tubercles which on each plate are supplemented usually by 2 smaller, internal tubercles. Small granules occur irregularly among the internal tubercles.

The interambulacral plates are comparatively high with exceedingly large aureoles, which, particularly in the plates below the ambitus, are sub-quadrate in shape, as their margins follow closely the borders of the plates. Consequently the interambulacral midzone is narrow, less than half of the width of the aureoles. The aureoles are moderately incised and are not confluent. The bosses rise well above the level of the test to the prominent smooth tubercles, the perforations of which tend to be elongated in the direction of the vertical axis of the test. Outside the prominent well-shaped tubercles of the scrobicular circle, the narrow adradial and admedian zones are covered by small closely spaced tubercles.

None of the sutures is incised although the median interambulacral suture tends to be depressed.

RADIOLES: A detached radiole lies across the type specimen (Pl. XXI, fig. 2). This can be confidently identified as belonging to this species. Similar radioles are known from Aldinga, and also other localities.

The radioles are massive and cylindrical, often with flattened distal terminations, and exceed the h.d. of the test (the longest known is that illustrated by Chapman and Cudmore *loc. cit.*, which, although broken, reaches over 10 cm in length). The shaft is ornamented by sparse, distant, projecting thorns which lack serial arrangement, although this may obtain to a slight extent in the flattened distal portion of the shaft, where smaller granules may also be present between the thorns. The collar is often as long as the width of the shaft at the neck, and expands markedly to the prominent milled ring. The neck is usually short but this appears to be variable. Portion of a dense coat of cortical hairs is preserved on some of the radioles (Pl. XXI, fig. 8). This extends a short distance up the thorns of the shaft. Where the hairs are perished the surface of the cortex is slightly dimpled. In transverse section (Fig. 2b) the radial lamellae are seen to be regular, the cortex layer comparatively thick and the thorns made up of extensions of the cortex layer.

MEASUREMENTS: The lectotype test has the following measurements: h.d. 75 mm; v.d. 32 mm; diameter of apical system *c.* 22 mm; diameter of peristome *c.* 22 mm. 7 interambulacral plates in each vertical column and 16 ambulacral plates opposite the highest interambulacral plates.

SYNOPSIS OF MATERIAL:

'Aldinga', Port Willunga Beds, Janjukian to Batesfordian: lectotype test; P19297, P19302 (test fragments); P19563-8 (radioles).

'Airey's Inlet', Point Addis Limestone, Janjukian, P18829 (radiole).

'Allot. 14, Par. Wataepoolan' (?Wataepoolan Limestone, Loc. XXVI, Brown 1958, p. 13), CPC 4813 (radiole), ?Janjukian.

'Waurn Ponds', Waurn Ponds Limestone, P19676-83 (radioles), Janjukian or Longfordian.

RANGE: The species is probably confined to the Janjukian and Longfordian. Jenkins (1958) indirectly records '*Prionocidaris*' from the Bochara Limestone, Hamilton, of Batesfordian age. This, however, is poorly founded.

REMARKS: Chapman and Cudmore described this form as a species of *Prionocidaris*, considering the pores to be conjugate. This condition was fulfilled by the inclusion of an interambulacral zone of *Phyllacanthus duncani* in their type material, and of all other test fragments of *P. duncani* from the Gambier Limestone in the species.

This difficulty in distinguishing *P. duncani* and *S.* (?) *scoparia* is understandable, for the tests of the two species are very similar in their general features (large size, narrow interambulacral midzone and the simple ornament of the narrow interporiferous tract). Moreover, *S.* (?) *scoparia* possesses ridged scrobicular tubercles similar to those of *Phyllacanthus*. However, interambulacral plates of *S.* (?) *scoparia* may be distinguished as the scrobicular tubercles overhang the more incised and larger, sub-quadrate aureoles. The non-conjugate pores of *S.* (?) *scoparia* distinguish the ambulacra, and further, prevent the species from being placed in *Prionocidaris*.

Undoubtedly the main character which led Chapman and Cudmore to consider

this as a species of *Prionocidaris* was the ornament of the radioles. Even so, the short neck and long collar with the prominent, expanded milled ring are features unlike those of *Prionocidaris* and recall rather *Stylocidaris*. But the species cannot be regarded as typical of *Stylocidaris* for the coarse ornament of the radioles is unlike that of any living species of the genus. Furthermore, the spongy coat of anastomosing cortical hairs, seen on some of the radioles, is a feature foreign to *Stylocidaris* for in this genus the cortical hairs are normally simple. A further atypical feature is the specialized scrobicular tubercles which recall those of *Phyllacanthus*. Probably this species should be set apart as a separate genus having no nearer relative than *Stylocidaris*. It bears no obvious comparison with any other adequately known fossil species.
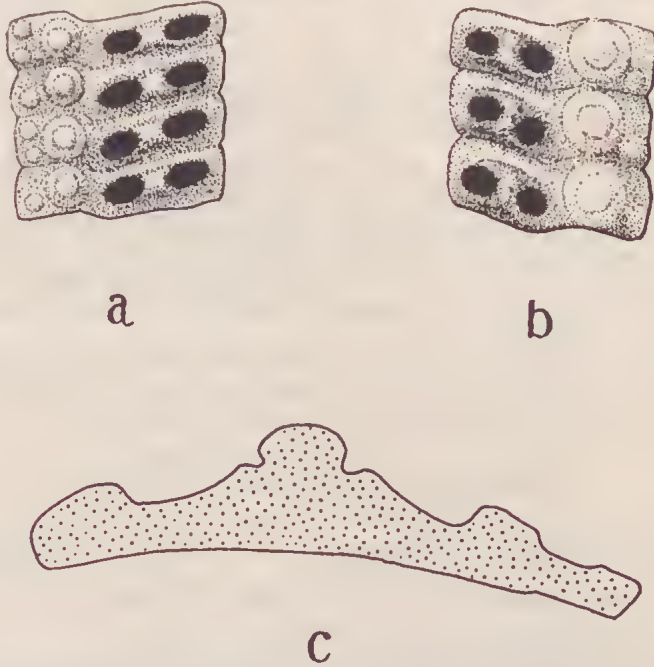

a   b

c

Fig. 1—*Stylocidaris* (?) spp. a, *Stylocidaris* (?) *scoparia* (Chapman & Cudmore). Enlargement of ambital ambulacrum of lectotype (AUGD T360), × 10. b-c, *Stylocidaris* (?) *chapmani* sp. nov. b, Enlargement of ambital ambulacrum of holotype (P18908), ×10. c, Profile of ambulacral and interambulacral plates (P18911), × 6.

The removal of *scoparia* from *Prionocidaris* raises the question of whether the genus can be said to occur in the Tertiary of Australasia. Fell (1954) named two species of *Prionocidaris, P. haasti* from the Duntroonian and *P. marshalli* from the Bortonian of New Zealand. Both of these species were based on radioles, and the former was regarded as belonging to a species of *Prionocidaris* largely because of similarity with the radioles of *S.* (?) *scoparia*. That *P. marshalli* probably has kinship with the Histocidarina will be discussed in Part II.

It does seem, however, that *Prionocidaris* was represented in the Tertiary of the Indo-Pacific. Mortensen (1928, p. 436) has suggested that the Eocene *Leiocidaris canaliculata* Duncan and Sladen (1884, p. 109-112, Pl. 21, fig. 1-9), from Western Sind, may be a species of *Prionocidaris*. The specimen figured as such by Davies

(1943, Pl. 11, fig. 1) from the Shekan Limestone of the Kohat-Potwar Basin (BM E32392) has been examined and found to possess the test characters of *Prionocidaris*. Furthermore, some radioles from the upper Miocene and Pliocene of Java and the Aru Islands have been placed in the living species *P. baculosa* (Lamarck) by Jeannet and Martin (1937). I have also examined a fragmentary test (CPC 4814) from the Miocene of Lagaba Island, Papua, which is best regarded as belonging to a species of *Prionocidaris*.

Stylocidaris (?) sp. cf. S. (?) scoparia (Chapman & Cudmore)

(Pl. XXI, fig. 3)

Stereocidaris australiae (Duncan), Chapman and Cudmore 1934, p. 127-130 (*partim*), (*non*) fig.
Prionocidaris scoparia Chapman and Cudmore 1934, p. 134-135 (*partim*), (*non*) fig.
(*Non*) *Leiocidaris Australiae* Duncan 1877, p. 45, Pl. 3, fig. 1-2.

MATERIAL AND HORIZON: 'Point Flinders, Aire Coast', P19597-602, P19752-7 (radioles), Lower Glen Aire Clays, 'Pre-Janjukian'.

DESCRIPTION AND REMARKS: These radioles closely resemble those of *S.* (?) *scoparia* in their long collars and spinose ornament of the shafts. They differ most obviously in their smaller size, the more closely spaced and often longer thorns which show a tendency to be arranged in longitudinal series. They probably are from a form closely related to *S.* (?) *scoparia*, but, in the absence of knowledge of the test characters, this cannot be properly established. The radioles are known only from the one locality.

These radioles were identified in the collection as *Stereocidaris australiae* (Duncan) although their museum label reads—'These may include *Prionocidaris*; and on these specimens that genus is recorded in our paper, F.A.C.'.

Stylocidaris (?) chapmani sp. nov.

(Pl. XXII, fig. 6-8; Fig. 1 b-c, 2a)

Stereocidaris australiae (Duncan), Chapman and Cudmore 1934, p. 127-130 (*partim*), (*non*) fig.
Stereocidaris australiae (Duncan), H. L. Clark 1946, p. 290 (*partim*); Fell 1954, p. 10-11 (*partim*).
(*Non*) *Leiocidaris Australiae* Duncan 1877, p. 45, Pl. 3, fig. 1-2.

DIAGNOSIS: Test moderately large with 5 interambulacral plates in each column, with the scrobicules of the upper plates of each column somewhat reduced in size. Aureoles not sunken; interambulacral midzone marked by transverse grooves.

Interporiferous tract with a regular series of marginal tubercles, and usually 2 smaller internal tubercles on each plate.

Radioles large, generally flattened and distally expanded. Shaft ornamented by small thorn-like denticles arrayed on longitudinal ridges.

TYPE SPECIMEN: Holotype P18908, an interambulacral zone labelled '*Stereocidaris australiae*', from the 'lower beds', AW. 5 (probably the Brown's Creek Clays at Castle Cove, of 'Pre-Janjukian' age).

DESCRIPTION: The incised ambulacra are sinuate and about $\frac{1}{5}$ the width of the interambulacra. The interporiferous tract is slightly narrower than the more sunken poriferous tract. The fairly large, almost contiguous marginal tubercles form a regular vertical series. A smaller internal tubercle is also present diagonally below the marginal tubercle on each of the larger ambulacral plates (Fig. 1b). The

rounded pores are slightly oblique and non-conjugate with the wall separating the pores rising to a prominent crest, whereas the transverse ridge above the pores is low.

5 interambulacral plates are present in each vertical column, with the aureoles of the upper plate of each column somewhat reduced in size. On the lower plates the aureoles are shallow, so that the prominent, smooth tubercles rise well above the level of the test. The aureoles, mounted slightly toward the adradial side of each column, are transversely oval below the ambitus, and those of the lowermost plates may become almost confluent. The scrobicular tubercles are fairly large and closely spaced so that only rarely is a small secondary tubercle interposed between them. The interambulacral midzone and the adradial zones of the plates are deeply channelled by sub-horizontal grooves, so that the small secondary tubercles appear to be mounted on ridges.

MEASUREMENTS: P18908 was derived from a test with the following inferred measurements: h.d. *c.* 40 mm; v.d. *c.* 20 mm; diameter of apical system *c.* 20 mm; diameter of peristome *c.* 15 mm; 15 ambulacral plates opposite the highest interambulacral plate.

ASSOCIATION OF TEST AND RADIOLES: In the collections from AW. 5 (Castle Cove) there are test fragments of 2 species, *Stylocidaris* (?) *chapmani* sp. nov. and *Stereocidaris australiae* (Duncan). Two groups of radioles also occur at this locality. The first group, described below, is associated with *S. chapmani* because:

(1) All available test fragments come from a fawn coloured clay (probably the Brown's Creek Clays) as do also all radioles of the first group. The second group are preserved in an impure limestone as are also all the test fragments of *S. australiae*.

(2) P18902 shows a radiole of the second group lying in close proximity to a few isolated interambulacral plates of *S. australiae* (Duncan).

DESCRIPTION OF RADIOLES: The radioles are comparatively long and slender, in length apparently approaching the h.d. of the test. They are usually distinctly flattened, so that even the collar may be ovate in cross-section. In general, the shafts expand distally and become progressively more flattened so that at their distal termination they may almost be 3 times the width at the neck. However, some of the radioles retain an almost cylindrical shape for most of their length. The shaft is ornamented by about 12 longitudinal series of small, distally directed thorns, which may increase in number to over 20 such series on the expanded, distal portions of the shafts. Proximally the small thorns are somewhat randomly placed. On well preserved spines a dense coat of thick, strongly-anastomosing cortical hairs can be seen, filling the interspaces between the thorns and in some cases almost enveloping the smaller ones (Pl. XXII, fig. 8). The neck is long, between about $\frac{1}{2}$ and $1\frac{1}{2}$ times the diameter of the shaft at the neck, while the length of the collar is about $\frac{3}{4}$ of this. The milled ring is slightly expanded and is marked by longitudinal striations, as is also the collar. The acetabulum shows no trace of crenulation.

SYNOPSIS OF MATERIAL:

'Lower beds, AW.5', Brown's Creek Clays, 'Pre-Janjukian', P18908, 10-11 (test fragments), P18914-36 (radioles).

REMARKS: The generalized test characters of this species indicate a relationship with Stylocidarina or the Cidarina. The most striking and characteristic feature of the species is seen in the flattened and distally expanded radioles. This feature, however, is seen in both these groups in *Cidaris blakei* (A. Agassiz) in the Cidarina,
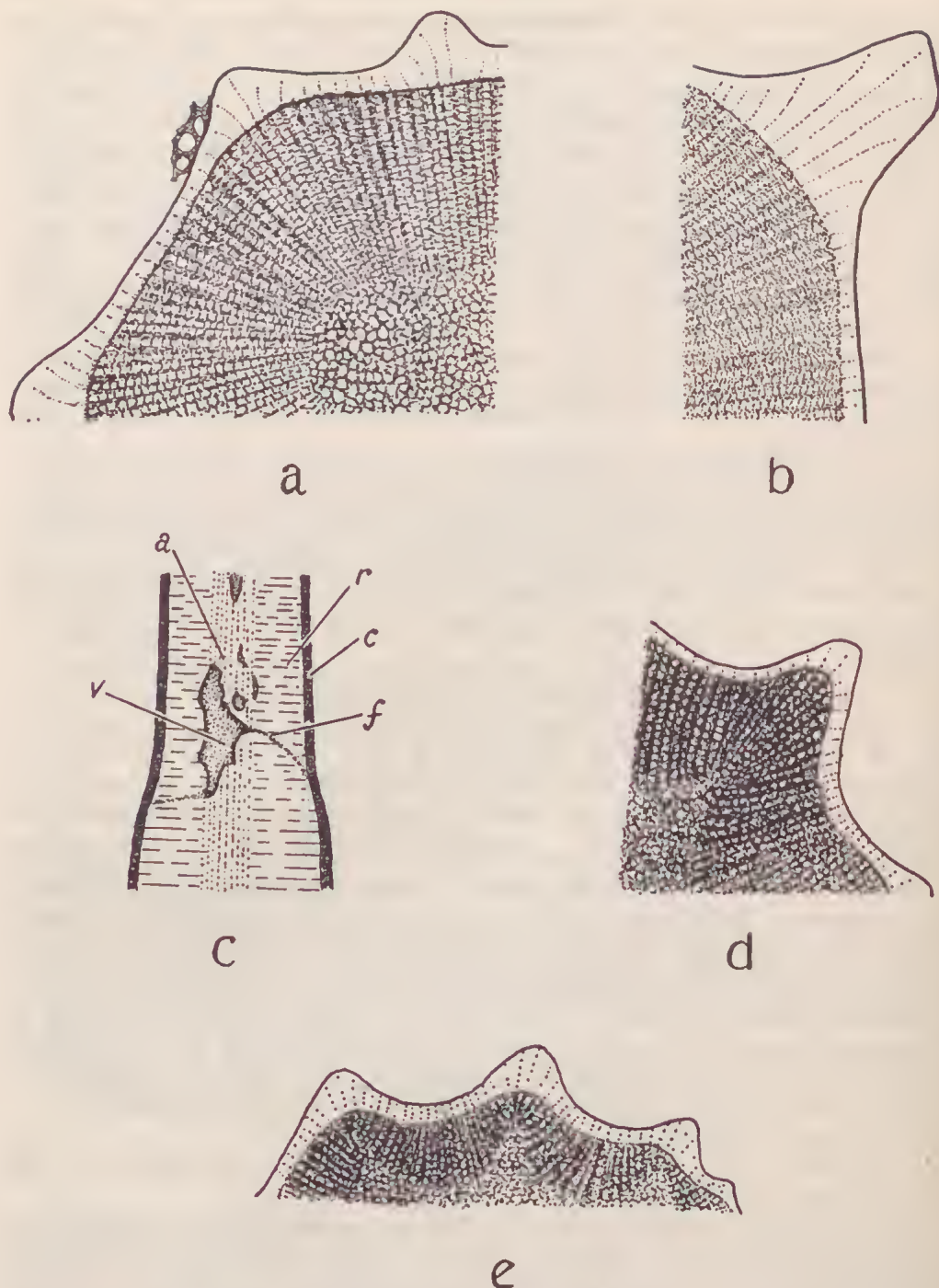
Fig. 2—Sections of cidarid radioles. a, *Stylocidaris* (?) *chapmani* sp. nov. Portion of transverse section (P18923), × 40. b, *Stylocidaris* (?) *scoparia* (Chapman & Cudmore). Transverse section of cortical layer (P19568), × 40. c-d, *Phyllacanthus clarkii* (Chapman & Cudmore). c, Polished longitudinal section of constricted radiole (P19684), *a* axial zone, *r* radial zone, *c* cortex, *f* fracture, *v* voids. × 10. d, Portion of transverse section from distal part of radiole, × 40. e, *Phyllacanthus serratus* sp. nov. Portion of transverse section from distal part of radiole (P19696), × 40.

and in the West Indian genus *Hesperocidaris* in the Stylocidarina, thus affording no indication of the broader affinities of the species, as would, perhaps, be expected.

From present knowledge of its features, one is tempted to place this species in the genus *Hesperocidaris*. However, the zoo-geographic implications which this identification would then suggest are most certainly not warranted from a form which can be identified only circumstantially. This same would apply were one to identify the species as belonging to *Cidaris* S.S. The most neutral procedure for the present, is to questionably refer the species to *Stylocidaris*.

Within the context of *Stylocidaris* it should be observed that this species could be construed as indicating that the genus *Hesperocidaris*—employed by Mortensen (1928) to include three very closely related West Indian 'species', and separated from *Stylocidaris* by the absence of a limb on the large globiferous pedicellariae, and the flattened radioles with the thick coat of anastomosing cortical hairs—is based on trivial features of no more than specific merit within the genus *Stylocidaris*.

<div align="center">

Genus Eucidaris Pomel (*sensu* Döderlein)

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Gymnocidaris A. Agassiz 1863, p. 17.
Eucidaris Pomel, Döderlein 1887, p. 42.
Eucidaris Pomel, Mortensen 1928, p. 384 *et seq.* (*cum synon.*).
Eucidaris Pomel, Fell 1954, p. 45; Cooke 1959, p. 8; Hertlein and Grant 1960, p. 102.
(*Non*) *Gymnocidaris* L. Agassiz 1838, p. 3 (*fide* Mortensen 1935, p. 406).
(*Nec*) *Eucidaris* Pomel 1883, p. 109.

TYPE SPECIES: The type species of *Eucidaris* Pomel is *Cidarites monilifera* Goldfuss, by the subsequent designation of Cooke (1959, p. 8). A re-examination of the type specimen of *Cidarites monilifera* Goldfuss is given elsewhere (Philip 1963) where it is concluded that the species is best included in the genus *Stereocidaris* Pomel. As it is intended that the problem of the application of the name *Eucidaris* Pomel should be laid before the International Commission for Zoological Nomenclature, the genus *Eucidaris* is employed here in the sense of Döderlein, H. L. Clark and subsequent authors.

DIAGNOSIS: Comparatively small forms with smooth tubercles and non-conjugate pores. Radioles short, cylindrical or fusiform, terminating with a small distal projection and with a short collar. Shaft ornamented with low rounded warts, arranged in longitudinal series, between which is a thick spongy coat of anastomosing cortical hairs.

DISTRIBUTION: Mortensen (1928) recognized 6 living species of *Eucidaris*. Mayr (1954, p. 3) notes that these illustrate 'geographic speciation almost diagrammatically' and that 'if all were considered as having the rank of subspecies only, the genus would be monotypic'. Mayr omitted from discussion the southern species *E. australiae* Mortensen (1950a, p. 291, Pl. 8, fig. 5-7) but in this form also, the distinctions are but slight.

As fossil the genus is known from the Neogene of California, Mexico and the West Indies (Grant and Hertlein 1938, Hertlein and Grant 1960, Jackson 1922). H. L. Clark (1945, p. 313) has described *Phyllacanthus tylotus* from the Pleistocene of Fiji, which species, as Fell (1954, p. 12) points out, may prove to be a species of *Eucidaris*. Cooke (1954) has identified a cidarid from the Pliocene of Okinawa as *Cidaris metularia*.

More ancient origins of the genus are suggested by the New Zealand occurrences. Fell (1954) described the two species, *Eucidaris coralloides,* based on a single radiole from the Whaingaroan, and *E. strombilata* based on radioles which range from the Upper Eocene (?) to the Waitakian.

O

The Australian radioles described below, while obviously distinct from this latter New Zealand species, are clearly very closely related. Consequently they are described as a sub-species of this form.

Eucidaris strombilata Fell

Eucidaris strombilata Fell 1954, 47-48, Pl. 8, fig. A, E, F, G, H, J; Pl. 10, fig. B; Pl. 11, fig. E.

Eucidaris strombilata felli subsp. nov.

(Pl. XXII, fig. 1-2, 5, 9)

'Club-shaped Spines, *incertae sedis*', Chapman and Cudmore 1934, p. 142, Pl. 14, fig. 25-26b.

DIAGNOSIS: Small club-shaped or fusiform radioles with the shaft often markedly widened and sharply constricted distally to a well developed terminal crown.

TYPE SPECIMEN: Holotype P19958, a radiole from Waurn Ponds, Waurn Ponds Limestone, Janjukian.

DESCRIPTION: These are comparatively small, club-shaped or fusiform radioles with the shaft constricted distally below a well marked terminal crown. The shaft is ornamented by rounded warts which are arranged in longitudinal series or may be mounted on longitudinal ridges. These warts tend to be larger on one side of the radiole. Both the poorly delimited neck and the collar are short, and the milled ring is only slightly expanded. Between the warts of the surface of the shaft are remnants of a thick coat of spongy cortical hairs.

MEASUREMENTS: P19958 (holotype): length 10 mm, maximum width of shaft 3 mm.

SYNOPSIS OF MATERIAL:

'Waurn Ponds', Waurn Ponds Limestone, P19958-62, Janjukian.
'$\frac{1}{2}$ mile S. Lethbridge' (? T.M. 3), 'Lower Maude Beds', P18540-2, Janjukian or Longfordian.
'Airey's Inlet', Point Addis Limestone, P18830-1, Janjukian.
'Par. Mageppa, Pte. Bore Allot. 10, 171-180', GSV 58906, ? Janjukian.

RANGE: Janjukian and ? Longfordian.

REMARKS: Radioles which belong to this subspecies are abundantly represented in material from Boonaya, near Balladonia, W.A. Almost a thousand such radioles are in the collections of the National Museum, Melbourne. Consequently, a further account of this subspecies, particularly of the variation in these radioles, will be given elsewhere in a description of the Tertiary echinoids of Western Australia.

These radioles were originally described and figured by Chapman and Cudmore (*loc. cit.*) as 'Club-shaped Spines, *incertae sedis*', with the suggestion that they could belong to a species of *Eudicaris*. Fell (1954, p. 11) recognized their undoubted affinities, and listed this form as *Eucidaris* sp. nov. He further pointed to the main differences which exist between this and the New Zealand *E. strombilata*, namely 'the spine having a much wider and more sharply truncated form in the Australian specimens'.

No test fragments which could belong to this subspecies have been recognized.

Genus Phyllacanthus Brandt

Phyllacanthus Brandt 1835, p. 67.
Leiocidaris Desor 1855, p. 48.
Phyllacanthus Brandt, Mortensen 1928, p. 500 *et seq.* (*cum synon.*).

Phyllacanthus Brandt, Fell 1954, p. 48-9.
(*Non*) *Phyllacanthus* Brandt, Cooke 1941, p. 3; 1959, p. 10-12.
(*Nec*) *Leiocidaris* auctt.

TYPE SPECIES: *Cidarites* (*Phyllacanthus*) *dubia* Brandt, the designation validadated in Opinion 208, International Commission on Zoological Nomenclature. The type species of *Leiocidaris* Desor is *Cidarites imperialis* Lamarck, designated by de Loriol (1873, p. 63).

DIAGNOSIS: Large, thick-tested forms with prominent smooth tubercles. Scrobicular tubercles conspicuous and characteristically ridged. Apical system dicyclic with widely exsert oculars and with the madreporite markedly enlarged. Peristome wide, usually considerably wider than the apical system. Pores sub-conjugate with marginal tubercles of the ambulacra well developed.

Radioles large and robust, cylindrical or fusiform, with shaft covered by fine granules, usually arranged in longitudinal series, particularly distally, where they form longitudinal ridges. Cortical hairs short and anastomosing. Cortical layer thick with the radial laminae usually arising in fan-like bundles from the axial zone.

REMARKS: There has been a tendency among palaeontologists to use the genus *Leiocidaris* Desor as a form genus to include species with smooth tubercles and conjugate pores (Jeannet 1931, 1933, etc.). Although this practice has been condoned by Mortensen (1932, p. 177) it leads only to confusion, for *Leiocidaris* is a direct synonym of *Phyllacanthus*. An extension of this practice is seen in the work of Cooke (1941, 1959) who uses *Phyllacanthus* as a form genus in a sense similar to *Leiocidaris* as used by other authors. However, the genus *Phyllacanthus*, as defined by Mortensen, is a well-characterized genus with a number of morphological peculiarities of both test and radioles which allow the recognition of the genus in fossil material with a considerable degree of assurance. It is a strictly Indo-Pacific genus, well represented in the Recent Australian fauna, and ranging back into the Oligocene of Australasia. The basis for Fell's (1953, p. 248) statement that '*Phyllacanthus* . . . had already become established in northern India in the Eocene' is obscure.

DISTRIBUTION: Mortensen (1928) recognized 6 living species, and subsequently (1936) added a further species from Indian waters. 4 of the species are confined to the Australian coast, but their distribution and variation are poorly known. 3 species groups are apparently present in the genus. *P. imperialis* (Lamarck) is widely distributed throughout the Indo-Pacific and has the geographic variant *P. dubius* (Brandt) from the Bonin islands. In Australian waters, *P. imperialis* is known only from Torres Strait. From elsewhere in Australian waters 3 other species have been described, which, although standing very close together, may well all be merely geographic variants of *P. imperialis*. These are:

P. parvispinus (Woods) from the E. Australian coast.

P. magnificus H. L. Clark off Geraldton, W. A.

P. irregularis Mortensen from the S. Australian coast. Cotton and Godfrey (1942, p. 216, Pl. 12) have proposed the subspecies *kimberi* for the local South Australian variety of *P. irregularis*.

Apart from these stand *P. longispinus* Mortensen from Northern Australia, and *P. forcipulatus* Mortensen from the Indian Ocean, both apparently representing well marked species probably sympatric with the *P. imperialis* group.

Fossil radioles, and more rarely test fragments, which may be included in the genus are known from Cainozoic rocks throughout much of the Indo-Pacific and Australasian regions. These include:

Phyllacanthus imperialis (Lamarck), Cottreau 1908, p. 183-4, Pl. 5, fig. 10. 'Couches à Lepidocyclines' Madagascar. From the same horizon Cottreau illustrated (Pl. 5, fig. 8) a fragmentary spine he identified as '*Cidaris* cf. *striato-granosa* d'Archiac, 1850' (? 1847). Although this specimen lacks any of the distinctive features of *Phyllacanthus* (its distal portion is missing) the ornament of the shaft closely resembles that of the contemporaneous Australian Batesfordian species *P. duncani.* Of Cottreau's other species of *Phyllacanthus* from the Miocene of Madagascar, his *Phyllacanthus* sp. (Pl. 5, fig. 7-7a) certainly is not a *Phyllacanthus,* but apparently affords the basis for the record of the genus *Chondrocidaris* in the Miocene of Madagascar, while his *Phyllacanthus verticillatus* (Pl. 5, fig. 9-9a) resembles very closely the living species '*Plococidaris*' *verticillatus* (Lamarck). [The type species of the genus *Plococidaris* Mortensen is *Cidarites bispinosa* Lamarck, by the original designation of Mortensen (1909, p. 51). *C. verticillata* Lamarck was also included in the genus. In 1928, Mortensen removed the species *bispinosa* to the genus *Prionocidaris,* but retained the name *Plococidaris* for the species *verticillata.* Subsequent authors have followed Mortensen.] Similar radioles are known from the Pliocene of East Africa and the Miocene of India (Currie 1930, Pl. 16, fig. 7 (*partim*) ; Duncan and Sladen 1882, Pl. 45, fig. 1-12).

Phyllacanthus sp. Currie 1930, p. 178, Pl. 16, fig. 8, from the Pliocene and Pleistocene of coastal Kenya.

Phyllacanthus imperialis (Lamarck) Forteau 1904, from Quaternary deposits near Suez (*fide* Mortensen 1928, p. 509).

From the Miocene Gáj Series of Western Sind, Duncan and Sladen (1885, Pl. 44, fig. 13-13a) illustrate a 'large cylindrical spine of the character of *Phyllacanthus imperialis* or *P. dubius*'. Mortensen (1928, p. 509) considered that this probably represented some species of *Phyllacanthus.* Duncan and Sladen's *Cidaris opipara* (*op. cit.* p. 279-81, Pl. 44, fig. 1-8), based on test fragments from the same horizon, could also very well be a *Phyllacanthus.* The ambulacral pores are subconjugate in the manner of *Phyllacanthus* and closely resemble those of *P. duncani* described below (cf. Duncan and Sladen's fig. 2 and fig. 3c), the peristome is much wider than the apical system (cf. Duncan and Sladen's fig. 1 and 3), but the figures give no indication that the peculiar scrobicular tubercles typical of *Phyllacanthus* are present. It seems very likely, however, that *C. opipara* is a species of *Phyllacanthus.*

From Miocene and younger sediments of the East Indies, a number of *Phyllacanthus* radioles have been described. These include:

Phyllacanthus imperialis (Lamarck) Jeannet and R. Martin 1937, p. 222, from the Middle Pliocene of East Java.

Phyllacanthus dubius Brandt, Jeannet and R. Martin 1937, p. 223, fig. 5, from the Upper Miocene and Middle Pliocene of Java.

Phyllacanthus javana K. Martin 1885, p. 289, Pl. 15, fig. 294; *Phyllacanthus imperialis* var. *javana* K. Martin, Jeannet and R. Martin 1937, p. 222-3, fig. 4, from the Upper Miocene of Java. This form was recorded from the Miocene of Yule Island, New Guinea, by Chapman and Cudmore (1930). Radioles in the Commonwealth Palaeontological Collection (CPC 4815-6), thus labelled, belong to a species of *Phyllacanthus.*

Phyllacanthus dubius var. *sundiaca* R. Martin *in* Jeannet and R. Martin 1937, p. 223-4 (*non Phyllacanthus sundaica* K. Martin 1885, p. 287, Pl. 15, fig. 293a-c) from the Lower Miocene of Java.

The radioles figured by Currie (1924, Pl. 4, fig. 20, 22) from the Pliocene of

Aru Island, although resembling *Phyllacanthus* spines, were identified as *Priono-cidaris baculosa* by Jeannet and Martin (1937, p. 220).

Cidaris (Phyllacanthus) imperialis (Lamarck) Abrard 1946, p. 19-20, Pl. 1, fig. 18, from the Upper Miocene of the New Hebrides.

Phyllacanthus imperialis (Lamarck) is reported by H. L. Clark (1945, p. 312-5) as occurring in rocks from Lower Miocene to Pleistocene age in Fiji. Clark (*op. cit.* p. 313, Pl. 41, fig. D) also described a Pleistocene species *Phyllacanthus tylotus* but, as Fell (1954, p. 12) points out, the radiole concerned does not appear to have belonged to a species of *Phyllacanthus* and may well be a species of *Eucidaris*.

From New Zealand 2 Tertiary species have been described. These are:

Phyllacanthus titan Fell 1954, p. 49-51, Pl. 1B, 3, 10A, 11D, from rocks of Upper Oligocene to Middle Miocene age in New Zealand.

Phyllacanthus wellmanae Fell 1954, p. 51-3, Pl. 1C-D, 2, from the uppermost Miocene of New Zealand.

Thus, *Phyllacanthus* is a strictly Indo-Pacific and Australasian genus, not only in its present-day distribution but also in its Cainozoic occurrences.

Perhaps the genus is even more ancient in origin. Whitehouse (1924) illustrated a broken cidarid radiole from the Bajocian of Western Australia as *Cidaris* sp. This, the only described Jurassic echinoid from Australia, possesses surface ornament extremely reminiscent of *Phyllacanthus*. Whitehouse's Pl. 1, fig. 1b is reproduced here as Pl. XXIV, fig. 4 for comparison with *P. duncani* (Pl. XXIV, fig. 5).

There is no adequately substantiated record of the genus outside of the Indo-Pacific province. Its occurrence in the E. United States of America (Cooke 1941, Fisher 1951, Cooke 1959) is based on the Upper Eocene species *Cidaris mortoni* Conrad. This was placed in the genus *Phyllacanthus* 'because the pores in each pair are distant and connected by a groove' (Cook 1941, p. 4-5). Cooke's figures of the species shows the pores to be fully conjugate, so that the species lacks all the features which allow recognition of *Phyllacanthus* in fossil material.

Sanchez Roig (1949) has described some Tertiary and Cretaceous cidarids from Cuba, among which he diagnosed several new species of *Phyllacanthus* and *Leiocidaris*. The descriptions and figures of these are such that all but their most general features are obscure; none of them would seem to bear any relationship to *Phyllacanthus*. The same applies to all the cidarids described in this paper, and for this reason they are not discussed further.

MORPHOLOGY: Although most authors have described the pores of *Phyllacanthus* as conjugate, they really do not fulfil this condition in the usual sense of the term. Mortensen, for example (1928, p. 505), has some hesitation in using the term to describe the relation of the pores in *P. imperialis*. In *Phyllacanthus* the upper part of the wall between the pores is strongly raised to form a sub-triangular protuberance. This narrows and is truncated by a shallow groove below so that the lower parts of the pores are connected (Fig. 5). This condition is different from the more normal condition of conjugation as seen, for example, in *Prionocidaris*, in which the pores lie in a groove which has the same height as the pores. It is preferred to confine the term 'conjugate' to this latter condition, whilst the term 'subconjugate' is used for the arrangement which appears to be consistently developed in *Phyllacanthus*. It may be noted that the pore relationship in species of other genera may be similar (eg. *Stylocidaris brevicollis* (de Meijere) and also some species of *Eucidaris*).

Fell (1954) found that the conjugation was less marked in the New Zealand Oligocene species *P. titan,* an observation which led him to the conclusion that the species 'is related to some more generalized non-conjugate ancestor, from which the Phyllacanthids descend' (p. 53). While this cannot be gainsaid, it should be observed that all traces of conjugation can be lost on even slightly worn specimens. Well preserved specimens of *P. duncani* from sediments of Janjukian age in E. Australia show an arrangement of pores indistinguishable from that of the living species of *Phyllacanthus.*

Another peculiarity which distinguishes the test of *Phyllacanthus* is the remarkable specialization of the scrobicular tubercles. Each of these possesses a well-defined ridge running from the mamelon across the boss to the edge of the scrobicule of the primary tubercle. The outer side of the boss of each scrobicular tubercle is also raised in a wider, more poorly defined complementary ridge (Fig. 4b, 5d). The ridges would seem to inhibit the movement of the flattened scrobicular spines in the direction of the primary tubercle around which they are mounted.

Although in living cidarids scrobicular tubercles of this nature are apparently confined to *Phyllacanthus* Mortensen (1928, p. 388, fig. 113a) illustrates a similar internal ridge for the scrobicular tubercles of *Eucidaris metularia,* and states that 'the mamelon is somewhat prolonged toward the aureole' (p. 387). A similar structure is also noted in *E. thouarsii.* The ridges, however, are much less strongly developed than those of *Phyllacanthus,* and lack the outer elevation. A number of fossil species have been illustrated which at least possess the inner ridge of the scrobicular tubercle. These principally include 2 species groups of *Stereocidaris* which will be discussed in Part II. Also Mortensen (1928, p. 501) considered that *Cidaris lacrymula* Duncan and Sladen (1882, Pl. 1, fig. 1-7) from the Cretaceous of Sind possessed this feature, but Duncan and Sladen (p. 8) describe the scrobicular tubercles as 'tear-shaped' which suggests they may be of a character different from those of true *Phyllacanthus.*

Among the Australian Tertiary species similar scrobicular tubercles are seen in *Stylocidaris* (?) *scoparia,* although here the ridges are but poorly defined and the tubercles overhang the aureoles.

Although Fell (1954) mentions this character as occurring in the scrobicular tubercles of his *Phyllacanthus titan,* his drawing of the interambulacral plates of this species (Pl. 3E) shows their arrangement to be peculiar, for a ridge is shown which becomes progressively narrower away from the mamelon and may even fade before the outer margin of the well-defined boss of the scrobicular tubercle is reached. The mamelons of the scrobicular tubercles appear to strongly overhang the aureoles so that the inner ridges are not seen.

Mortensen (1928, p. 502) pointed out that the appearance of a *Phyllacanthus* radiole in transverse section is fairly characteristic, as the radial laminae arise in fan-like bundles from the axial zone. Fell (1954, p. 30) writes that, 'Even a small fragment [of a *Phyllacanthus* radiole] can be identified by the transverse section, which is characteristic'.

It would seem, however, that a certain caution is necessary in using this character to identify the genus. Even in species in which the character is well marked, the fan-like bundles in the radial zone become progressively developed distally, so that in the proximal part of the radiole they may not be at all obvious (eg. *P. titan* Fell 1954, cf. Pl. 10 A, B). Among living cidarids the feature is not confined to

Phyllacanthus. It is seen in *Prionocidaris baculosa* (Lamarck) and in *Compso-cidaris pyrsacantha* Ikeda (1939b, Pl. 9, fig. 3), a form closely related to *Stereo-cidaris,* and a comparable arrangement is developed in *Eucidaris clavata* Mortensen (1928, p. 410, fig. 121). Among fossil forms the same structure is seen in the radioles of *Cidaris farringdonensis* Wright and *C. punctata* Römer (Hesse 1900), which species, as Mortensen (1928, p. 502) points out, do not in other respects recall *Phyllacanthus.*

REMARKS ON THE AUSTRALIAN TERTIARY SPECIES: Fragments of *Phyllacan-thus,* both radioles and test remains, are probably the most widely distributed and abundant of any of the cidarid genera represented in the Tertiary of Australia. Chapman and Cudmore placed all the *Phyllacanthus* radioles in the one species, although they included *Phyllacanthus* tests in the type material of their species of *Prionocidaris* and *Chondrocidaris.* Here 5 taxonomic groupings are recognized, consisting of 3 species, 2 of which possess 2 subspecies distinguished by the character of the radioles.

Because of the wide range of variation ascribed by Chapman and Cudmore to their *Phyllacanthus duncani,* Fell (1954) found comparison of his New Zealand species with their Australian contemporaries difficult. A brief comparison of some features of the tests given in Table 2 shows the New Zealand forms to represent distinct, although probably closely related species. Other features, such as the

TABLE 2

Species	No. interamb. plates in a column	Interporiferous tract	Interamb. midzone
AUSTRALIA			
P. duncani	6 (7)	narrow	narrow
P. clarkii	9	wide	wide
NEW ZEALAND			
P. titan	?	wide	intermediate
P. wellmanae	9	narrow	wide

confluent scrobicules of the lower interambulacral plates in *P. wellmanae,* further point to the difference of the New Zealand forms.

The thick test and large spines of *Phyllacanthus* are particularly robust fossils. A remanić origin is quite possible for some of the worn fragments which occur in the younger Tertiary horizons. Instances in which worn remains only are known are noted in the occurrences given below.

No specimens so labelled have been examined from the following localities from which Chapman and Cudmore (1934) list their *Phyllacanthus duncani*: Green Gully, Keilor; Bowker's Steps, Princetown; First cliff N. of 'Britana', 3 miles below Morgan, upper Beds; Curlewis, locality Ad 12 or 13; Cape Barren Islands, Bass Strait.

Phyllacanthus duncani Chapman & Cudmore

Phyllacanthus duncani Chapman and Cudmore 1934, p. 131-133 (*partim*), fig. (*partim*).

DIAGNOSIS: A moderately large species of *Phyllacanthus* with up to 6 (7) inter-ambulacral plates in each vertical series. Interambulacral midzone typically narrow, and covered by coarse secondary tubercles. Interporiferous tracts narrow, with large marginal tubercles on each ambital plate usually augmented by 2 smaller in-ternal tubercles arranged in a vertical series.

Radioles stout and cylindrical or gently tapering; apparently only rarely exceeding the h.d. of the test.

REMARKS: The specimens available are divisible into 2 well-marked groups (described as subspecies) on the character of the radioles; test fragments associated with both types are identical, so that the subspecies can be identified only somewhat circumstantially. As the radioles of one group are known only from the Gambier Limestone (and W. Australia) all test fragments of *P. duncani* from this formation are identified as belonging to the second subspecies *P. duncani gambierensis* subsp. nov. Full synonymies and descriptions are given below under each form.
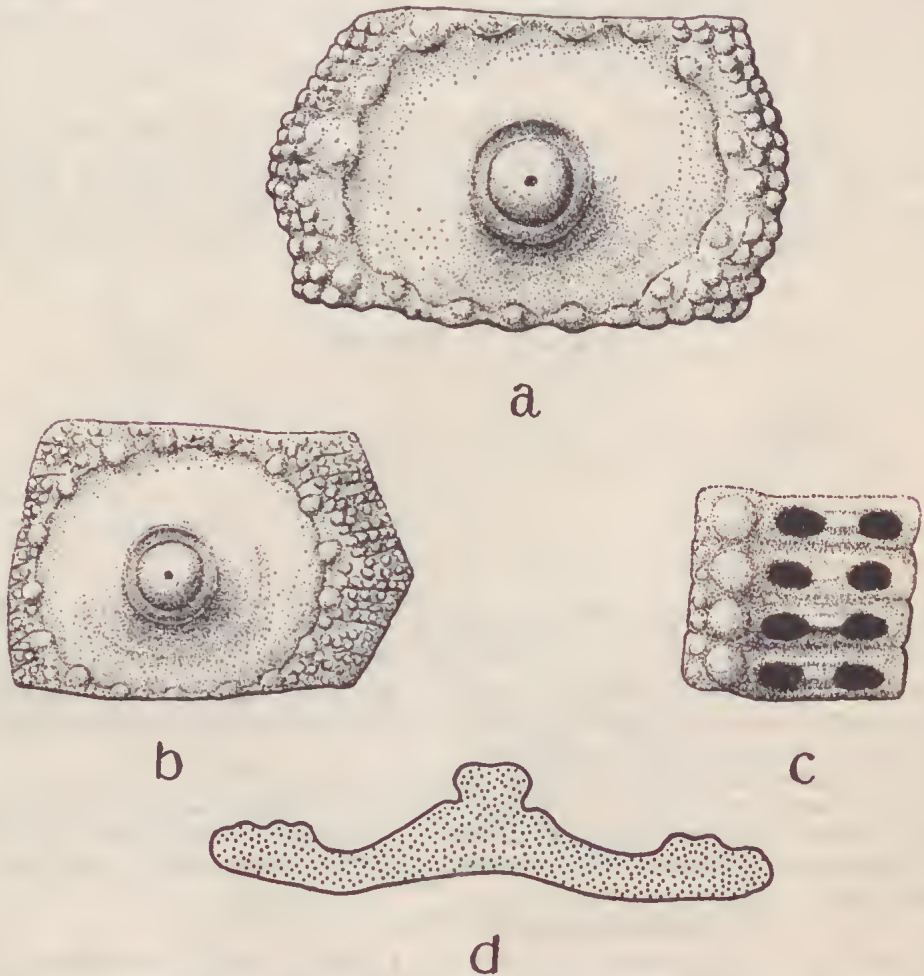

Fig. 3—*Phyllacanthus duncani duncani* Chapman & Cudmore. a, Ambital interambulacral plate (P19781), × 4. b, Ambital interambulacral plate of holotype (P13707), × 4. c, Enlargement of ambital ambulacrum of holotype × 12. d, Profile of broken interambulacral plate (P19608), × 4. (Interambulacral plates worn so that ridged scrobicular tubercles not apparent in these figures.)

Phyllacanthus duncani duncani Chapman & Cudmore

(Pl. XXII, fig. 3-4; Pl. XXIII, fig. 1, 3-4, 6-9, 12-14; Pl. XXIV, fig. 5-14; Fig. 3)

Leiocidaris sp. nov. Duncan 1887, p. 412.
?? *Balivina hentyana* Chapman 1916, p. 145-146, fig. 1
Phyllacanthus duncani Chapman and Cudmore 1934, p. 131-134 (*partim*), Pl. 12, fig. 7-8; Pl. 15, fig. 33 (5 radioles), (*non*) Pl. 12, fig. 9.
Stereocidaris australiae (Duncan) Chapman and Cudmore 1934, p. 127-130 (*partim*), (*non*) fig.; H. L. Clark 1946, p. 290 (*partim*); Fell 1954, p. 10-11 (*partim*).
Phyllacanthus duncani Chapman and Cudmore, H. L. Clark 1946, p. 282 (*partim*); Fell 1954, p. 11 (*partim*).
(*Non*) *Leiocidaris Australiae* Duncan 1877, p. 45, Pl. 3, fig. 1-2.
(*Nec*) *Balivina hentyana* Chapman *auctt.* (*fide* Jenkins 1958).

DIAGNOSIS: A form of *Phyllacanthus duncani* with radioles ornamented with comparatively large, closely spaced granules which are arranged in longitudinal series usually for most of the length of the shaft.

TYPE SPECIMEN: Holotype P13707, designated by Chapman and Cudmore (1934, p. 133, p. 148), 'Batesford Limestone' (no locality), Batesfordian.

DESCRIPTION: The ambulacra are narrow (about 16% of the width of the interambulacra) and slightly sinuate. The interporiferous tracts are slightly narrower than the sunken poriferous tracts, with prominent marginal tubercles forming regular vertical series. Toward the ambitus each ambulacral plate is further ornamented by 2 smaller internal tubercles which form an inner vertical series. The pores are typically subconjugate.

Usually 6 interambulacral plates are present in each vertical column. The large shallow aureoles, mounted toward the centre of each column, are rounded on the few uppermost plates, but adorally they become transversely ovate. The uppermost tubercle of each interambulacral zone may be rudimentary. On the other plates, the primary tubercles are large and prominent and the bosses rise well above the test to the wide smooth platforms on which are mounted the large mamelons. The scrobicular tubercles are prominent, rarely with secondary tubercles interposed. The interambulacral midzone is usually very narrow ($c.$ $\frac{1}{8}$ of the width of the zone) but in some specimens may be much wider ($c.$ $\frac{1}{6}$ of the width of the zone). The secondary tubercles of the adradial zone and midzone are generally very coarse and consequently not abundant, but this again is variable.

MEASUREMENTS: The following estimates of dimensions may be made from P19787, one of the only interambulacral zones in which both the adapical and adoral terminations are complete: h.d. 43 mm; width of peristome 22 mm; width of apical system 17 mm; up to 19 ambulacral plates opposite the highest ambital interambulacral plates.

ASSOCIATION OF TEST AND RADIOLES: The radioles of this species are in no case known directly associated with the test. The radioles described below as belonging to *P. duncani duncani* occur with the test fragments at a number of localities and horizons (eg. Batesford, Flinders Limestone, Lower Maude Beds, Point Addis Limestone, Waurn Ponds Limestone) where tests of no other species of *Phyllacanthus* are known to be present, so they may be associated with a considerable degree of confidence.

DESCRIPTION OF RADIOLES: The radioles are thick and cylindrical, with the shaft gently tapering. The neck and collar are both low, never exceeding the diameter of the shaft and usually about half this. The shafts of the large radioles are ornamented with between 24 and 28 longitudinal series of coarse rounded granules.

Proximally these tend to become deranged and more random while distally they coalesce to form longitudinal ridges in which the granules are represented by slight nodes. The interspaces between the granules are covered with short anastomosing cortical hairs. There is a certain amount of variation in the size of the granules, which may be separated from their neighbours by interspaces of between about half and twice their diameter in the proximal portion of the spine. The milled ring and collar are in general longitudinally striate, with the diameter of the milled ring usually about 1·5 times the diameter of the shaft, but in some radioles from Batesford (Pl. XXIV, fig. 7) the diameter of the milled ring may be expanded to twice that of the shaft. The transverse section is typical of *Phyllacanthus*.

The maximum length of the radioles appears to have rarely exceeded the h.d. of the test. The largest spine in the collection is 70 mm long while the largest test fragment in the collection would have had a similar h.d.

SYNOPSIS OF MATERIAL:

Port Willunga Beds and equivalents:
'Seaford', AUGD 15743 and one other test fragment *ex* R. L. Foster Coll.; 'Lower Beds, Aldinga', P19265-71; 282-3; P19787 (test fragments).

Point Addis Limestone, Janjukian:
'Airey's Inlet', P18811-28 (radioles).

Waurn Ponds Limestone, Janjukian or Longfordian:
'Waurn Ponds', P19674-5 (radioles).

'A.W.3, i.e. Calder River Limestone, Janjukian:
P18993-19004 (radioles); P19569-77 (radioles).

'A.W.4', ? Calder River Limestone, Janjukian:
P19013-5 (radioles); ? P19016-22 (radioles—locality uncertain).

Lower Maude Beds, Janjukian or Longfordian:
'½ mile S. of Lethbridge on left bank of stream' (? S.E., ? T.M.3; Singleton 1941, p. 71, fig. 12), P18482-530 (test fragments and radioles); 'T.M. 1, 2, 4', P20011-7 (radioles); 'T.M.3', P20007-10 (radioles).

Table Cape, Tasmania, Janjukian:
'*Crassatella*' Beds, P19725-9 (radioles); P19662-70 (radioles).

'Alkemade's Quarry, right bank of Porcupine Cr., Kawarren'. P 19145-53 (radioles), ? Janjukian.

'Pte Bore, Allot. 10, Par. Mageppa, 171-180', GSV 58907 (worn radioles), ? Janjukian.

'Allots. 1 & 2, Par. Sandford, Sandford Limestone', GSV 57436 (worn radioles), ? Janjukian.

'Allot. 14, Par. Wataepoolan' (? Wataepoolan Limestone; Brown's (1958), p. 13) locality XXVI), CPC 4817 (radioles and test fragments), ? Janjukian.

Batesford Limestone, Batesfordian:
No locality, P13706 (paratype), P13707 (holotype), P13708 (5 radioles figured as paratypes by Chapman and Cudmore, Pl. 15, fig. 33), P19780-3 (test fragments). Middle Quarry, P19629-36 (radioles). Filter Quarry, P19607-28 (radioles and test fragments). Upper Quarry, P19516-20 (radioles).

Flinders Limestone, Flinders, Batesfordian:
P19912-4 (2 worn interambs. and 1 radiole); P20089-92 (radioles); P20081-8 (radioles); P19419-25 (radioles and test fragments); P20094-8 (test fragments); P13864 (test fragments).

'Orphanage Hill', Fyansford Clay, P19758-60 (3 extremely worn and pitted radioles which could well have been derived from older horizons), Balcombian.

? 'Marl pit, 250 yds, W. Brook's Quarry, Glencoe', Gippsland Limestone, GSV 58908 (test fragment), Batesfordian.

? 'Clifton Bank, Muddy Creek', Hamilton Beds, P19455-8 (isolated interambulacral plates), Balcombian.

'Beneath nodule bed, Beaumaris', P22303 (test fragment), ? Balcombian.

The Glencoe test fragment (Pl. XXIII, fig. 5) and the small interambulacral plates from Clifton Bank (Pl. XXIII, fig. 11) may be of a different form. The Glencoe specimen differs from *P. duncani* in that the ambulacral plates are larger, and fewer are opposite each interambulacral plate. Another difference, seen particularly in the specimens from Clifton Bank, is that the primary tubercle is relatively smaller than in typical specimens of *P. duncani*. However, very little can be stated positively of the relationships of these immature and incomplete specimens.

REMARKS: The holotype of this species differs markedly from the other available test fragments in:

(1) A wider interambulacral midzone which is covered by smaller and more numerous horizontally aligned secondary tubercles.

(2) There would seem to have been more interambulacral plates (7, or perhaps 8) than is typical.

So distinctive is the holotype that it was originally thought to be a species different from the remainder of the material. A thorough re-examination of all the specimens has convinced me that this separation cannot be upheld; other specimens do show a tendency toward the development of a wide interambulacral midzone, and a large specimen from the Gambier Limestone (P13709—Chapman and Cudmore's second syntype of *Prionocidaris scoparia*, and figured *op. cit.* Pl. 12, fig. 11), belonging to the subspecies *gambierensis*, permits the interpretation of 7 interambulacral plates in each vertical column. Undoubtedly Chapman and Cudmore chose this atypical specimen as the holotype of their *P. duncani* because they included specimens of *P. clarkii* (Chapman and Cudmore) in the species, and so were able to have a type to some extent intermediate between the two.

The name *hentyana* may eventually prove to be applicable to this form. Jenkins (1958) has pointed out that the much recorded Victorian foraminiferal species *Bolivina hentyana* Chapman, originally described from the Red Limestone of Muddy Creek (i.e. the Bochara Limestone), is based on either the miliary or scrobicular spine of a cidarid. Jenkins quotes a letter from Professor H. B. Fell thus—'The type illustrated in Chapman's paper looks like a miliary (or perhaps scrobicular) spine of a cidarid, and in particular resembles *Phyllocanthus* and *Prionocidaris*; both genera are present in beds from which it comes' (*sic*). Fell apparently was also sent similar topotype radioles which Jenkins quotes were identified as the scrobicular spines of 'either *Phyllocanthus* or *Prionocidaris*, probably the former'. This would imply that generic characters may be found in the secondary radioles of cidarids, which certainly is not the case.

Chapman and Cudmore (1933) list neither *Phyllacanthus duncani* nor their '*Prionocidaris*' *scoparia* from the Bochara Limestone, and the present collection contains neither species from this horizon. As Professor Fell has kindly written (6. iii. 61) to say he has no knowledge of Jenkins's paper, the implied record of these species from the Bochara Limestone for the present lacks foundation.

Of the radioles illustrated by Jenkins, it may be pointed out that if they were from a species of *Phyllacanthus*, then they were derived from a remarkably immature specimen. The problem of the application of the name *hentyana* may be

satisfactorily resolved at some future date by the discovery of the complete test with
attached radioles, or perhaps even a painstaking investigation of the cidarid re-
mains from the Bochara Limestone.

Duncan's (1887, p. 412) *Leiocidaris* sp. nov. is based on an interambulacral
zone partially obscured by matrix (BM E197). There are 6 interambulacral plates
in each column, the interporiferous tracts of the ambulacra are narrow and the
specimen is fully typical of *P. duncani*. However, this specimen is given as coming
from Bairnsdale (i.e. Bairnsdale Limestone) whence the species is not otherwise
known, but where *P. clarkii* occurs in abundance. Until further material substan-
tiates this occurrence, the record must be treated with caution.

Two radioles in the collection (P19612, P19000) show evidence of the work of
an unknown boring organism. In P19612 (Pl. XXIII, fig. 7) the surface granules
which rise above the cortical hairs are pierced by one, 2 or even 3 minute circular
holes averaging about ·07 mm in diameter. The fact that the borings appear to be
confined to the granules and do not extend onto the collar and base of the radiole
suggests that the borings were made during the life of the cidarid. P19000, a worn
spine from AW.3, appears to possess similarly disposed holes. Records of the
occurrence of boring parasites in cidarid radioles appear to be rare. Grönwall
(1900) has reported the occurrence of much coarser borings in the Cretaceous
Tylocidaris vexilifera, which again appear to have been formed during the life of
the echinoid (Mortensen 1928, p. 42). Koehler (1926) records the occurrence of
parasitic gastropods infesting the primary radioles of the living species *Stylocidaris
tiara,* but in this case the spines abort and form galls. The only comparable borings
which appear to have been reported would seem to be those mentioned briefly and
figured by Bather (1909, p. 181, Pl. 11, fig. 334) in the Triassic species '*Cidaris*'
dorsata marginata Bather.

The expanded milled ring, present in some of the radioles from Batesford, is of
interest (Pl. XXIV, fig. 7). Similar expansion is known in the radioles of the
genus *Homalocidaris,* but there the feature is consistently developed (in the 2
specimens known) and so it was considered by Mortensen (1928, p. 137) to be a
generic attribute. As this expansion presumably can be correlated with an excessive
development of the muscles of the radioles, in *P. duncani* it probably should be
interpreted as a change induced by environment.

Cidaris opipara Duncan and Sladen (1885, p. 279-281, Pl. 44, fig. 1-8), from
the Miocene Gáj Series of Western Sind, could represent a species almost identical
with *P. duncani* should it prove to be a species of *Phyllacanthus.* The only distinc-
tion which can be seen from the published information is that *C. opipara* possesses
a slightly wider, more sparsely tuberculated interambulacral midzone. However,
if the *Phyllacanthus* radiole illustrated from the same horizon (Duncan and Sladen
op. cit. Pl. 45, fig. 13-13a) belongs to *C. opipara,* then *P. duncani* will differ ob-
viously in the character of the radioles. Cottreau (1908, Pl. 5, fig. 8) has illustrated
a fragmentary radiole identified as '*Cidaris* cf. *striato-granosa* d'Archiac' from the
Miocene of Madagascar, the ornament of which closely resembles that of the
radioles of *P. duncani duncani,* but the Madagascar radiole need not have belonged
to a species of *Phyllacanthus.* The same may also be said of the cidarid radiole
illustrated by Whitehouse (1924, Pl. 1, fig. 1; enlargement of surface detail re-
produced here as Pl. XXIV, fig. 4) from the Bajocian of Western Australia, but
here the comparison is even more striking.

Phyllacanthus duncani gambierensis subsp. nov.

(Pl. XXIII, fig. 2, 10; Pl. XXIV, fig. 1-3; Fig. 4)

Phyllacanthus duncani Chapman and Cudmore 1934, p. 131-133 (*partim*), (*non*) fig.
Prionocidaris scoparia Chapman and Cudmore 1934, p. 134-135 (*partim*), Pl. 12, fig. 11. (*non*)
Pl. 12, fig. 10; Pl. 15, fig.
Stereocidaris australiae (Duncan) Chapman and Cudmore 1934. p. 127-130 (*partim*), (*non*)
fig; H. L. Clark 1946, p. 290 (*partim*); Fell 1954, p. 10-11 (*partim*).
Phyllacanthus duncani Chapman and Cudmore, H. L. Clark 1946, p. 282 (*partim*); Fell 1954, p.
11 (*partim*).
Prionocidaris scoparia Chapman and Cudmore, H. L. Clark 1946, p. 286 (*partim*); Fell 1954, p.
11 (*partim*).
(*Non*) *Leiocidaris Australiae* Duncan 1877, p. 45, Pl. 3, fig. 1-2.

DIAGNOSIS: A form of *Phyllacanthus duncani* with radioles ornamented by small, widely spaced granules which show little tendency to be arrayed in longitudinal series.

TYPE SPECIMEN: Holotype P19525, 'Railway Ballast Quarry, $7\frac{1}{2}$ miles NNW. of Mount Gambier Town', Gambier Limestone, ? Janjukian.

DESCRIPTION: The radioles are thick and tapering, but with a slight tendency for the shaft to be expanded to reach its maximum diameter 10 mm or so above the neck. The acetabulum, milled ring and collar are all slightly worn in the available speci-
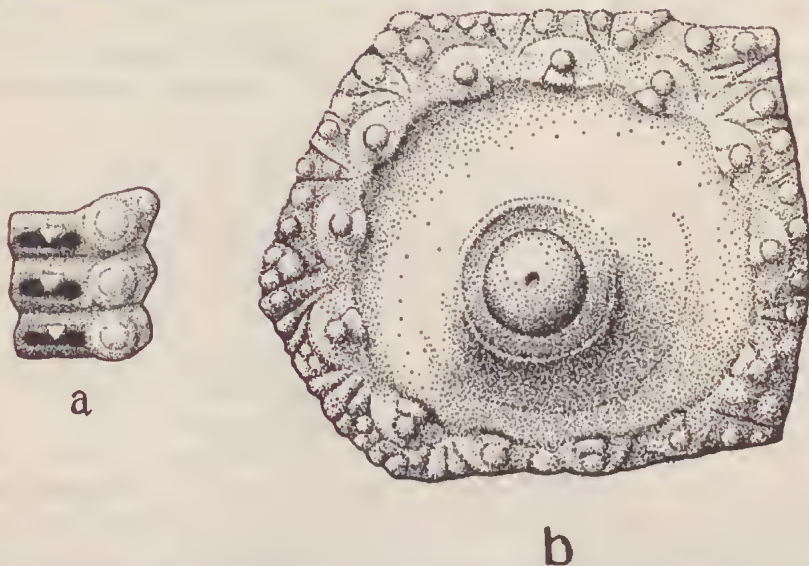

Fig. 4—*Phyllacanthus duncani gambierensis* subsp. nov. a, Upper ambulacral plates showing simplified ornament (P19604), × 12. b, Upper interambulacral plate of same. × 6.

mens. The neck is short, usually about half the diameter of the shaft or less. The shaft is ornamented by small, well-spaced granules which are arranged in poorly defined longitudinal series which are separated by interspaces of about 3 or 4 times the width of the granules. The extremities are missing from all the available spines, but there appears to be little tendency for the granules to become confluent distally to form longitudinal ridges. The interspaces between the granules are covered by short anastomosing cortical hairs (Pl. XXIV, fig. 3).

MEASUREMENTS: Holotype: length 47 mm; maximum width of shaft 5·1 mm; width of collar 4·8 mm.

SYNOPSIS OF MATERIAL:

Gambier Limestone, ? Janjukian:

'Railway Ballast Quarry, 7½ miles NNW. of Mount Gambier Town', P19521-32 (test fragments and radioles including holotype).

Test fragments of *P. duncani* from the Gambier Limestone probably belonging to this subspecies:

Nelson, P19604-6; 'Knight's Siding Railway Quarry', near Mount Gambier, P19367-8 and P13709 (syntype of *Prionocidaris scoparia*, illustrated by Chapman and Cudmore 1934, Pl. 12, fig. 11).

13 radioles from Western Australia will be described elsewhere.

REMARKS: Chapman and Cudmore identified the batch of material including the type specimen (9 radioles and 3 test fragments) as '*Stereocidaris* and ? *Priono-cidaris*'. As they identified all the test fragments of *Phyllacanthus duncani* from the Gambier Limestone as *Prionocidaris*, it may be inferred that the radioles were re-garded by them as belonging to *Stereocidaris*, attesting to their distinctiveness. However, Chapman and Cudmore identified identical radioles from W. Australia as *Phyllacanthus duncani*.

The test fragments which are associated with the radioles at the type locality and which occur elsewhere in the Gambier Limestone, are identical with those of *P. duncani*. In the absence of any suggestion to the contrary, all the test fragments of *P. duncani* from the Gambier Limestone are placed in *P. duncani gambierensis*.

P. duncani gambierensis apparently represented a geographic or ecologic variant of the typical *P. duncani*.

Phyllacanthus clarkii (Chapman & Cudmore)

Chondrocidaris clarkii Chapman and Cudmore 1934, p. 141-142 (*partim*), fig. (*partim*).

DIAGNOSIS: A species of *Phyllacanthus* with up to 9 interambulacral plates in each vertical column. Interambulacral midzone wide, and covered by fine secon-dary tubercles arrayed in horizontal series. Interporiferous tracts comparatively wide, with 2 vertical series of small internal tubercles inside the large, regular marginal series.

Radioles (not known from the type horizon) expanded above the neck, and taper distally; apparently in length they usually exceed the h.d. of the test.

REMARKS: The test on which Chapman and Cudmore based their *Chondro-cidaris clarkii* belong to the second common Australian Tertiary species of *Phyllacanthus*. The lectotype (chosen below) possesses an enlarged peristome, sub-conjugate pores and the typical scrobicular tubercles of *Phyllacanthus*. Moreover, radioles associated with identical test fragments from various localities in Gipps-land are also fully characteristic of the genus. The radioles from Morgan, originally associated with the *Phyllacanthus* tests in the 'species' *Chondrocidaris clarkii*, will be discussed in Part II. Chapman and Cudmore met the requirement of pore con-jugation for their species of both the genera *Chondrocidaris* and *Prionocidaris* by including *Phyllacanthus* tests in their type material.

Again, 2 subspecies are recognizable in the material, based on the character of the radioles, and full synonymies are given under each form.

Phyllacanthus clarkii clarkii (Chapman & Cudmore)

(Pl. XXV, fig. 3, 5-8; Pl. XXVI, fig. 1, 3-4, 6-8; Fig. 2c-d, 5a-b, d-e)

Chondrocidaris clarkii Chapman and Cudmore 1934, p. 141-142 (*partim*), Pl. 13, fig. 15-17, (*non*) Pl. 15, fig. 31 (radioles).

Phyllacanthus duncani Chapman and Cudmore 1934, p. 131-133 (*partim*), (*non*) fig.; H. L. Clark 1946, p. 182 (*partim*); Fell 1954, p. 11 (*partim*).
Chondrocidaris clarkii Chapman and Cudmore, H. L. Clark (1946, p. 284 (*partim*); Fell 1954, p. 11 (*partim*).

DIAGNOSIS: A moderate sized form of *P. clarkii* with radioles ornamented by small and variably spaced granules, usually regularly arranged in longitudinal series on the distal half of the shaft, and forming continuous ridges towards the termination.

TYPE SPECIMEN: The lectotype of *Chondrocidaris clarkii* here chosen is P13159, the syntype test from 'Murray River Cliffs, below Overland Corner, Lower Beds' (Morgan Limestone, Batesfordian and Balcombian) and figured by Chapman and Cudmore 1934, Pl. 13, fig. 16-17.

DESCRIPTION OF LECTOTYPE: This is a complete test, with the apical system missing.

The ambulacra are narrow (about 15% the width of the interambulacra) and slightly sinuate. The interporiferous tracts are relatively wide, about the same width as the poriferous tracts, which are only slightly sunken. The large marginal tubercles of each plate form a regular vertical series. Toward the ambitus each of the ambulacral plates bears small internal tubercles arranged in 2 vertical series, but adorally and adapically only one such vertical series is present. The pores are typically subconjugate, although their detailed arrangement is not clear.

9 interambulacral plates are present in each complete column visible. The shallow aureoles, mounted toward the centres of the column, are rounded on the upper few plates, but become transversely ovate adorally. The primary tubercle is rudimentary on the smallest adapical interambulacral plate of each zone. On the other plates the boss is large and prominent, rising well above the level of the test to the smooth platform. The scrobicular tubercles, although prominent, are relatively smaller than those of *P. duncani*, and possess the characteristic inner ridge and outer elevation of their bosses. The interambulacral midzone is wide (about 20% of the width of the interambulacra) and covered by small secondary tubercles arranged in subhorizontal series. The median suture is slightly sunken and the horizontal sutures, particularly the upper ones, tend to be bare.

MEASUREMENTS: The lectotype has the following measurements: h.d., 59 mm; v.d. 32 mm; width of apical system 23 mm; width of peristome (inferred) 27 mm. There are 15 or 16 ambulacral plates opposite the highest ambital interambulacral plate.

ASSOCIATION OF TEST AND RADIOLES: No *Phyllacanthus* radioles from the type locality have been discovered in the various collections examined. Chapman and Cudmore (1934, p. 133) do record their *Phyllacanthus duncani* from the Morgan Limestone, but their specimens have not been located. The description of the radioles given below is based on material from the younger horizons of Bairnsdalian and Cheltenhamian age in Gippsland, where radioles occur together with test fragments identical with those from the Morgan Limestone. The discovery of radioles from the type horizon may necessitate the separation of the Gippsland form from *P. clarkii clarkii*.

DESCRIPTION OF RADIOLES: The radioles are thick and cylindrical, usually with an obvious swelling above the neck, from which the shaft tapers distally to an abrupt termination. The neck and collar are both short usually about half the diameter at the neck. The ornament of the shaft of the larger radioles is variable in the spacing of the small granules (cf. Pl. XXV, fig. 5; Pl. XXVI, fig. 8), which

may be 1-4 times their diameter apart on different radioles. Each granule is rounded in outline, but rises to a point which is directed distally. Between 24 and 40 longitudinal series of granules may be present on the proximal part of large radioles. The granules are normally somewhat randomly arranged on the proximal $\frac{1}{2}$ of the shaft, but are serially arranged distally, where they form continuous ridges for usually the distal $\frac{1}{4}$ of the shaft. The milled ring is usually only slightly expanded to less than $1\frac{1}{2}$ times the diameter at the neck. The transverse section is typical of *Phyllacanthus* (Fig. 2d).

SYNOPSIS OF MATERIAL:

Morgan Limestone, Batesfordian and Balcombian:
'Morgan', P19892-3 (test fragments), P13175 (Chapman and Cudmore's second syntype of *Chondrocidaris clarkii*, illustrated *op. cit.* Pl. 13, fig. 15); 'Murrary River Cliffs below Overland Corner, lower Beds', lectotype.
Bairnsdale Limestone and probable equivalents, Bairnsdalian:
'Cliff on left bank of Tambo River, 2 miles upstream from Swan Reach', P18398-404 (test fragments and radioles); 'Toorloo Creek, Toorloo Arm of Lake Tyers', P18365-75 (test fragments and radioles); 'Bairnsdale', P20108-19 (radioles), P4672-3 (test fragments); 'Yellow Limestone, Mitchell River opposite Bairnsdale', P19684-9 (radioles); 'Tramway cutting, Geol. Surv. Map.
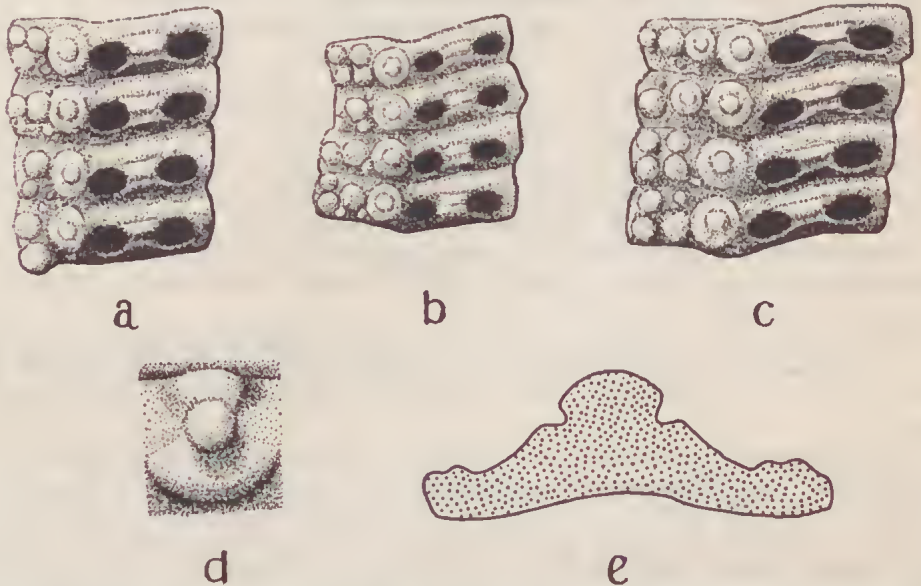

Fig. 5—*Phyllacanthus clarkii* (Chapman & Cudmore). a, Ambital ambulacral plates (P19892), × 15. b, Ambital ambulacral plates (P4672), × 10. c, Ambital ambulacral plates (P19166), × 10. d, Enlargement of ridged scrobicular tubercle (P18398), × 25. e, Profile of small interambulacral plate (P18398). a-b, d-e, *P. clarkii clarkii* (C. & C.); c, *P. clarkii impensus* subsp. nov.

Loc. 6' (i.e. Mississippi Creek), P18405-26 (radioles).
Tambo River Formation, Cheltenhamian:
'Road cutting on left bank of Tambo River, 100 yds S. of Swan Reach Bridge' P19044-66 (radioles).

Mordialloc Beds, Cheltenhamian:

'Loose in the shingle at Beaumaris', P19671-3 (3 worn radioles); 'Beaumaris', BM E17854-6 (radioles).

AUGD 15727, a test fragment of uncertain horizon from the St Vincent Basin sequence, belongs to *P. clarkii*.

REMARKS: One radiole from the Mitchell River (P19684; Pl. XXVI, fig. 4a) shows a peculiar distal constriction of the shaft. Currie (1924, Pl. 4, fig. 22) has illustrated a similarly constricted radiole from the Pliocene of the Aru Islands. (In fact, this and another of the radioles figured by Currie (fig. 20) strongly resemble those of *P. clarkii*, although there is no indication that the Aru radioles belong to *Phyllacanthus*.)

Undoubtedly one would consider these the result of rejuvenation after breakage, had not Mortensen (1928, p. 27-28) so categorically denied even the possibility of rejuvenated cidarid radioles. A longitudinal section of the radiole was ground to see if this could throw any light on the problem (Fig. 2c). This showed that, while the cortical layer is more or less continuous onto the constricted distal portion of the shaft (some of the outer longitudinal ridges are, some are not), there is a definite discontinuity within the zone of the radial lamellae. Within the axial 'medullary' region of the radiole are a number of irregular voids, the largest of which extends well into the radial zone along the discontinuity between the constricted and non-constricted portions of the shaft.

Thus a possible interpretation consistent with Mortensen's view is that the radiole was damaged or broken, but not to the extent that the distal portion was removed, or that the spine was shed by the animal. The tissue of the distal portion of the radiole became diseased and/or died (attested to by the voids) while the proximal portion continued to grow until ultimately the urchin died, or the radiole was shed. This explanation would be more convincing were the radiole from a Recent cidarid, in which the possibility of secondary effects could be ruled out.

Fell (1954, p. 51) records a test fragment from the Middle Miocene of Wepa Pass, New Zealand, which is apparently very close to *P. clarkii*. It is described as possessing similar ambulacra to *P. titan* Fell (i.e. the same as *P. clarkii*) and with a broader interambulacral midzone than is typical of that species.

Phyllacanthus clarkii impensus subsp. nov.
(Pl. XXV, fig. 9-10; Pl. XXVI, fig. 2, 5, 9; Fig. 5c)

Phyllacanthus duncani Chapman and Cudmore 1934, p. 131-133 (*partim*), Pl. 12, fig. 9 (*non*) fig. 7-8, (*non*) Pl. 15.
Phyllacanthus duncani Chapman and Cudmore, H. L. Clark 1946, p. 282 (*partim*); Fell 1954, p. 11 (*partim*).

DIAGNOSIS: A large form of *Phyllacanthus clarkii* with long tapering radioles, slightly expanded above the neck, and ornamented by very coarse, closely spaced granules lacking serial arrangement for most of the length of the shaft and coalescing in low ridges only close to the distal termination of the shaft.

TYPE SPECIMEN: Holotype radiole P19172, 'Beach at Port McDonnell, S.A., 300 yds easterly from the dune-rock cliffs west of the town, below high tide mark', Gambier Limestone, ? Longfordian.

DESCRIPTION: The radioles are massive, long and tapering with a slight swelling of the shaft immediately above the neck. The neck is short, never exceeding half the diameter of the shaft. The surface of the shaft is ornamented by extremely coarse rounded granules which are very closely mounted so that they are never separated

P1

by interspaces greater than their diameter. The granules are randomly arranged usually for well over half the length of the shaft, and form low ridges distally only for a very short distance. The interspaces between the granules are covered by short, anastomosing cortical hairs. The diameter of the milled ring is only slightly greater than that of the shaft. The transverse section is typical of *Phyllacanthus*.

The length of the radioles is apparently about 1·5 times the h.d. of the test. The largest radiole fragment has a length of 113 mm whereas the largest test fragment came from a test with a h.d. of approximately 80 mm.

Test fragments from the type locality, although considerably larger, are in all significant details identical with those for *P. clarkii clarkii*. A feature not seen in this subspecies, however, is that the secondary tubercles of the interambulacral midzone are all distinctly mamillate, but this would appear merely to attest to large size and fine preservation.

MEASUREMENTS: Holotype P19172, length (incomplete) 89 mm; width of neck 5 mm; maximum width of shaft 6 mm.

SYNOPSIS OF MATERIAL:

Gambier Limestone, at Port McDonnell, ? Longfordian:

P19162-73 (test fragments and radioles including holotype, perhaps all derived from one test), P13705 (a test fragment originally designated a paratype of *Phyllacanthus duncani* by Chapman and Cudmore 1934, and illustrated *op. cit.* Pl. 12, fig. 9), P13876 (test fragment of unknown locality, probably from the Gambier Limestone).

REMARKS: The radioles of this subspecies are the largest cidarid spines known from the Australian Tertiary rocks. They are longer than those of any living species of *Phyllacanthus* (74 mm for *P. imperialis* and 80 mm for the more slender spines of *P. longispinus*) and are almost comparable in length to the massive radioles of *P. titan* from the Oligocene of New Zealand. Fell (1954) estimates the length of these to be of the order of 200 mm, although the largest fragment available appears to have a length of 81 mm. The radioles of *P. clarkii impensus* appear to resemble closely those of *P. titan* although the test possesses a much wider interambulacral midzone. H. L. Clark (1946, p. 282) compared the test of this form, illustrated as *P. duncani* by Chapman and Cudmore, with *P. magnificus* because of this feature. This, however, is the only possible basis of comparison between the species.

Chapman and Cudmore (1934, p. 132) considered there to be 'four vertical rows of tubercles' on the interambulacral plates of the test of this subspecies (regarded as a 'senile' form of their *P. duncani*). This, although very rarely met with (Fig. 5c), is never consistently developed for the ambulacra are identical with those of *P. clarkii clarkii*.

The ornament of the radioles again affords the distinction between the two subspecies, although these are slightly expanded above the neck similar to those of *P. clarkii clarkii*, in contrast with those of *P. duncani* and *P. serratus* sp. nov. *P. clarkii clarkii* would seem to be descended from *P. clarkii impensus*. Fell (1954) notes that the radioles of his *P. titan* from older horizons 'have a more pronounced granulation of the cortex' than do those from the younger horizons. This suggests that a similar trend may be present in the New Zealand species.

Phyllacanthus serratus sp. nov.

(Pl. XXV, fig. 1-2, 4; Fig. 2e)

Phyllacanthus duncani Chapman and Cudmore 1934, p. 131-3 (*partim*), (*non*) fig.
Phyllacanthus duncani Chapman and Cudmore, H. L. Clark 1946, p. 282 (*partim*); Fell 1954,
    p. 11 (*partim*).

DIAGNOSIS: A form of *Phyllacanthus* with small uniformly tapering radioles, ornamented by longitudinally aligned granules which coalesce to form high, widely spaced ridges. The shaft has a definite serrated appearance.

TYPE SPECIMEN: Holotype P19691, 'Upper beds, Aldinga', i.e. Hallet Cove Sandstone of Middle Pliocene age.

DESCRIPTION OF RADIOLES: The radioles are small and cylindrical or with a gently tapering shaft. The neck and particularly the collar are long, with the neck usually slightly less than the diameter of the shaft, while the length of the collar may be over twice that of the neck. The shaft is ornamented proximally by between 14 and 20 longitudinally aligned rows of granules. These may be strongly aligned for the whole length of the shaft while distally they may form high ridges which may bear the granules. The granules are themselves high, and, although rounded in outline, rise to distally directed points which give a serrated appearance to the spine. Between the granules there is a spongy mass of fine cortical hairs. The transverse section (Fig. 2e), in which the radial lamellae arise in bundles from the axial zone, is fully typical of *Phyllacanthus*.

MEASUREMENTS: Holotype, length 25 mm; maximum width of shaft 3·5 mm; width at milled ring 3·8 mm.

SYNOPSIS OF MATERIAL:

'Upper beds, Aldinga', i.e. Hallet Cove Sandstone, P19690-8 (radioles), Middle Pliocene.

REMARKS: Chapman and Cudmore (1934) included these radioles from the Hallet Cove Sandstone in their first group of *Phyllacanthus* spines (i.e. with an expanded shaft above the neck—the group thus roughly corresponding with the radioles of *P. clarkii*). However, the small radioles do not belong here because they have uniformly tapering shafts, suggesting rather a comparison with *P. duncani*. Unlike *P. duncani*, however, the granules of the shaft rise to distally directed points and are much further separated (Pl. XXV, fig. 4). In the absence of knowledge of the test of this species nothing further can be said of its relationship to the other Australian Tertiary forms; it does seem likely that this form will prove to be a subspecies of one of the other Tertiary species.

The radioles are very different from those of any of the living Australian representatives of *Phyllacanthus*; however, *P. forcipulatus* Mortensen (1936, p. 307-9, Pls. 10-12), from the Indian Ocean, has almost as coarse longitudinal ridges on the radioles.

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Explanation to Plates

Figures × 1 unless otherwise stated

PLATE XXI

Fig. 1-2, 4-8—*Stylocidoris* (?) *scoporia* (Chapman & Cudmorc). (1) Test fragment P19297, 'Aldinga', Port Willunga Beds, × 2; (2) Adapical view of lectotype AUGD T360, 'Aldinga', Port Willunga Beds; (4) Ambital plates of lectotype, × 3; (5) Radioles P19565-7, Port Willunga Beds, 'Aldinga'; (6) Radiole CPC 4813, 'Allot. 14, Par. Wataepoolan', ? Wataepoolan Limestone, Janjukian; (7) Radiolcs P19676-8, 'Waurn Ponds', ? Janjukian; (8) Enlargement of shaft of radiole P19566, showing cortical hairs, 'Aldinga', Port Willunga Beds, × 5.

Fig. 3—*Stylocidoris* (?) sp. cf. *S.* (?) *scoporia* (Chapman & Cudmore). 4 radioles P19597-8, 19600, 19757, 'Point Flinders, Aire Coast', Lowcr Glen Aire Clays, 'Pre-Janjukian'.

PLATE XXII

Fig. 1-2, 5, 9—*Eucidoris strombiloto felli* subsp. nov. (1) Radioles P18540-2, 'Lcthbridge', ? Janjukian; (2) Radioles P18830-1, 'Airey's Inlet', Janjukian; (5) Holotype P19958, 'Waurn Ponds', Janjukian, × 5; (9) Large radiole GSV 58906, 'Pte Bore Allot. 10, Par. Mageppa', ? Janjukian, × 2.

Fig. 3-4—*Phyllacanthus dunconi* Chapman & Cudmore. (3) Test fragment P22303, 'Beneath nodule bcd, Beaumaris', ? Balcombian, × 3; (4) Interambulacral zone AUGD 15743 (*cx* R. L. Foster Coll.), 'Seaford', Port Willunga Beds, × 2.

Fig. 6-8—*Stylocidaris* (?) *chopmani* sp. nov. (6) Holotype P18908, 'lowcr beds, AW. 5', ? Brown's Creek Clays, 'Pre- Janjukian', × 2; (7) Radioles P18917, 24-26, 30-31, 'lower bcds, AW. 5'; (8) Surface detail of radiole P18915, showing the thick coat of strong anastomosing cortical hairs, 'lower beds, AW. 5', × 5.

PLATE XXIII

Fig. 1, 3-4, 6-9, 12-14—*Phylloconthus duncani dunconi* Chapman & Cudmore. (1) Test fragment P13864, 'Flinders', Batesfordian; (3) Isolated intcrambulacral platc P19426, 'Flindcrs', × 2; (4) Holotype P13707, 'Batesford'; (6) Test fragment P20097, 'Flinders'; (7) Radiole showing borings P19612, 'Batesford', × 5; (8) Test fragment P19782, 'Batesford'; (9) Isolated interambulacral plate P19607, with wide interambulacral midzone, 'Batesford', × 2; (12) Test fragment P19781, 'Batesford', × 2; (13) Test fragment P19787, 'lower beds, Aldinga', ? Port Willunga Beds; (14) Paratypc P13706, 'Batesford'.

Fig. 2, 10—*Phyllacanthus duncani gombierensis* subsp. nov. (2) Test fragment P19367; (10) Test fragmcnt P19368. Both from 'Quarry, Knight's Railway Siding, near Mt. Gambicr', ? Janjukian.

Fig. 5, 11—*Phyllacanthus duncani* Chapman & Cudmore (?) (5) Test fragment GSV 58908, '250 yds W. of Brock's Quarry, Glcncoe', Batesfordian, × 2; (11) Isolated interambulacral plate P19455, 'Clifton Bank, Muddy Creek', Balcombian, × 2.

PLATE XXIV

Fig. 1-3—*Phylloconthus dunconi gambierensis* subsp. nov. (1) Holotype P19525; (2) Radioles P19524, 26-28; (3) Surface dctail of holotypc, × 5. Specimens from '7½ miles NNW. of Mt Gambier', ? Janjukian.

Fig. 4—'*Cidaris*' sp. Enlargement of surface dctail of radiole from the Bajocian of Western Australia, × 6. (From Whitehouse 1924, Pl. 1, fig. 1b.)

Fig. 5-14—*Phyllocanthus dunconi dunconi* Chapman & Cudmore. (5) Surface detail of radiolc P19616, 'Filter Quarry, Batcsford', × 5; (6) Radioles P 19569-71, 'AW. 3', Janjukian;

(7) Radioles P19629-30 with expanded milled rings, 'Middle Quarry, Batesford'; (8) Radioles P18811-2, 'Airey's Inlet', Janjukian; (9) Radioles P18487-8, '½ mile S. of Lethbridge', ? Janjukian; (10) Radioles P19662-3, 'Lower Beds, Table Cape', Janjukian; (11) Radioles P19145-6, 'Kawarren', ? Janjukian; (12) Radiole P20081, 'Flinders', Batesfordian; (13) Radioles P19516-8, 'Upper Quarry, Batesford'; (14) Radioles P19611-6, 'Filter Quarry, Batesford'.

Plate XXV

Fig. 1-2, 4—*Phyllacanthus serratus* sp. nov. (1) Radioles P19690, 92-95; (2) Holotype P19691; (4) Surface detail of holotype, × 5. Specimens from the Middle Pliocene Hallet Cove Sandstone at Aldinga.

Fig. 3, 5-8—*Phyllacanthus clarkii clarkii* (Chapman & Cudmore), (3) Lectotype test P13159, 'Lower Beds, Murray River Cliffs, below Overland Corner', ? Balcombian; (5) Shaft of radiole P18400, 'Tambo River Cliff', Bairnsdalian, × 5; (6) Test fragment P19892, 'Morgan', ? Balcombian, × 2; (7) Test fragment AUGD 15727, 'Aldinga', ? Port Willunga Beds, × 2; (8) Test fragment P4672, 'Bairnsdale', Bairnsdalian.

Fig. 9-10—*Phyllacanthus clarkii impensus* subsp. nov. (9) Test fragment P19166, 'Port McDonnell', Gambier Limestone, ? Longfordian horizons; (10) Enlargement of same, × 2.

Plate XXVI

Phyllacanthus clarkii (Chapman & Cudmore)

Fig. 1, 3-4, 6-8—*Phyllacanthus clarkii clarkii* (C. & C.). (1) Radioles P19044-9, 'Road cutting downstream from Tambo Bridge', Cheltenhamian; (3) Radioles BM E17854-6, 'Beaumaris', Cheltenhamian; (4a) Constricted radiole P19684; (4b) radiole P19685, 'Bairnsdale', Bairnsdalian; (6) Radioles P18405-7, 'Tramway Cutting Loc. 6', Bairnsdalian; (7) Radioles P18366-7, 'Toorloo Creek', Bairnsdalian; (8) Shaft of radiole with closely spaced cortical granules, P19059, 'Tambo River', Bairnsdalian, × 5.

Fig. 2, 5, 9—*Phyllacanthus clarkii impensus* subsp. nov. (2) Radioles P19173; (5) Holotype P19172; (9) Shaft of radiole P19168, × 5. Specimens from 'Port McDonnell', Gambier Limestone, ? Longfordian horizons.